Revision of *Trophoniella* Hartman, 1959 (Polychaeta, Flabelligeridae)

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ABSTRACT

The identification and classification of flabelligerid polychaetes have been problematic due to three reasons: 1) the anterior end is rarely exposed and it carries the branchiae, whose type and arrangement are diagnostic; 2) there is no standardisation for naming chaetae; and 3) morphological delineations for most genera have been unstable. A redefinition and a revision of the type material of many species originally described in other genera but belonging to *Trophoniella* Hartman, 1959 are herein presented. *Trophoniella* together with *Piromis* Kinberg, 1856 and *Pycnoderma* Grube, 1877 share a very thick tunic and a projected branchial membrane which resembles a tongue. Their main difference is the type of neurochaetae in median and posterior chaetigers; thus, *Trophoniella* is redefined and restricted to include only the species with anchylosed hooks, whereas they are multiarticulated in *Piromis* and oligoarticulated in *Pycnoderma*; these two latter genera have been revised elsewhere. *Therochaetella* Hartman, 1967 is being regarded as a junior synonym of *Trophoniella*. The species of *Trophoniella* are further separated in two groups by the start of the anchylosed neurohooks (from about the chaetiger 10 or from median or posterior chaetigers). The species within each group can be separated by using the variation in the sediment cover and other attributes of noto- and neurochaetae. The genus as herein redefined contains, besides the type species, *T. avicularia* Caullery, 1944 from Indonesia, 26 species including 11 previously undescribed: *T. americana* (Monro, 1928) n. comb. from Galápagos and Panama, *T. bastidai* n. sp. from western Mexico, *T. borealis* (Hartman, 1965) n. comb. from northeastern South America, *T. capitata* (Nonato, 1966) n. comb. from Brazil, *T. chilensis* (Hartman, 1967) n. comb. from Chile, *T. ehlersi* (Day, 1973) n. comb. from the eastern United States, *T. eliasi* n. sp. from central Argentina, *T. enigmatica* n. sp. from the Mediterranean Sea, *T. fauveli* n. sp. from the Mediterranean Egyptian coast, *T. fernandensis* (Augener, 1918) reinstated, n. comb. from northwestern Africa, *T. fiegei* n. sp. from the Persian Gulf, *T. grandis* (Blanchard *in* Gay, 1849) n. comb. from central Chile, *T. harrisae* n. sp. from southern California, *T. havaica* (Kinberg, 1867) n. comb. from Hawaii, *T. hospita* (Fauchald, 1972) n. comb. from the Gulf of California, *T. incerta* (Augener, 1918) n. comb. from West Africa, *T. indica* (Fauvel,

1928) n. comb. from the Bay of Bengal, *T. jareckiorum* n. sp. from the Caribbean Sea, *T. lindae* n. sp. from the Caribbean Sea, *T. minuta* (Blanchard *in* Gay, 1849) n. comb. from Chile, *T. orensanzi* n. sp. from Uruguay, *T. reishi* n. sp. from the Gulf of California, *T. rigida* (Caullery, 1944) n. comb. from Indonesia, *T. rudis* (Grube & Müller *in* Grube, 1877) n. comb. from southern Brazil, *T. salazarae* n. sp. from western Mexico, and *T. tumbensis* (Hartmann-Schröder, 1962) n. comb. from Chile. Members of the species are marine and mainly tropical or subtropical, thriving in shallow bottoms.

KEY WORDS
Semiodera,
Trophoniella,
dorsal shield,
sediment cover,
anchylosed
neurochaetae,
new combinations,
new species.

RÉSUMÉ

Révision de Trophoniella *Hartman, 1959 (Polychaeta, Flabelligeridae).*

L'identification et la classification des polychètes flabelligériens ont été problématiques pour trois raisons : 1) l'extrémité antérieure est rarement exposée, alors qu'elle porte les branchies dont le type et l'arrangement sont des caractères de diagnose ; 2) il n'y a aucune standardisation pour nommer les types de soie ; et 3) les définitions morphologiques pour la plupart des genres ont été instables. Une redéfinition et une révision du matériel type de plusieurs espèces décrites originellement dans d'autres genres, mais appartenant à *Trophoniella* Hartman, 1959 sont présentées ici. Comme *Piromis* Kinberg, 1856 et *Pycnoderma* Grube, 1877, *Trophoniella* possède une tunique très épaisse et une membrane branchiale projetée qui ressemble à une langue. Leur différence principale est le type de neurochètes des sétigères des régions médiane et postérieure; *Trophoniella* est ainsi redéfini et a été restreint pour inclure seulement des espèces avec des crochets anchylosés, alors qu'ils sont multiarticulés chez *Piromis* et peu articulés chez *Pycnoderma*; ces deux genres ont été révisés dans un autre article. *Therochaetella* Hartman, 1967 est considéré comme un synonyme junior de *Trophoniella*. Les espèces de *Trophoniella* sont réparties en outre dans deux groupes par l'emplacement des premiers falcigères anchylosés (à partir du sétigère 10 environ, ou à partir des chaetigères médians ou postérieurs). Les espèces de chaque groupe peuvent encore être séparées en utilisant la variation dans la couverture sédimentaire et d'autres caractères de notochètes et neurochètes. Le genre comme redéfini ici contient, en dehors de l'espèce type, *T. avicularia* Caullery, 1944 d'Indonésie, 26 espèces, dont 11 nouvelles pour la science : *T. americana* (Monro, 1928) n. comb. des Galápagos et du Panama, *T. bastidai* n. sp. de l'ouest du Mexique, *T. borealis* (Hartman, 1965) n. comb. du nord-est de l'Amérique du Sud, *T. capitata* (Nonato, 1966) n. comb. du Brésil, *T. chilensis* (Hartman, 1967) n. comb. du Chili, *T. ehlersi* (Day, 1973) n. comb. de l'est des États-Unis, *T. eliasi* n. sp. du centre de l'Argentine, *T. enigmatica* n. sp. de la Méditerranée, *T. fauveli* n. sp. de la côte méditerranéenne égyptienne, *T. fernandensis* (Augener, 1918) reinstated, n. comb. du nord-ouest de l'Afrique, *T. fiegei* n. sp. du golfe Persique, *T. grandis* (Blanchard *in* Gay, 1849) n. comb. du centre du Chili, *T. harrisae* n. sp. du sud de la Californie, *T. havaica* (Kinberg, 1867) n. comb. de Hawaii, *T. hospita* (Fauchald, 1972) n. comb. du golfe de Californie, *T. incerta* (Augener, 1918) n. comb. d'Afrique de l'Ouest, *T. indica* (Fauvel, 1928) n. comb. de la baie du Bengale, *T. jareckiorum* n. sp. de la mer des Caraïbes, *T. lindae* n. sp. de la mer des Caraïbes, *T. minuta* (Blanchard *in* Gay, 1849) n. comb. du Chili, *T. orensanzi* n. sp. de l'Uruguay, *T. reishi* n. sp. du golfe de Californie, *T. rigida* (Caullery, 1944) n. comb. de l'Indonésie, *T. rudis* (Grube & Müller *in* Grube, 1877) n. comb. du sud du Brésil, *T. salazarae* n. sp. de l'ouest du Mexique, et *T. tumbensis* (Hartmann-Schröder, 1962) n. comb. du Chili. Ce sont toutes des espèces marines vivant principalement dans les eaux tropicales ou subtropicales peu profondes.

MOTS CLÉS
Semiodera,
Trophoniella,
bouclier dorsal,
couverture sédimentaire,
soies ventrales
anchylosées,
combinaisons nouvelles,
espèces nouvelles.

INTRODUCTION

The flabelligerid genera *Piromis* Kinberg, 1867, *Pycnoderma* Grube, 1877 and *Trophoniella* Hartman, 1959 are closely allied (Salazar-Vallejo *et al.* 2008). The species included in these three genera have a thick cuticle, often provided with sediment particles, their branchial filaments are sessile over a tongue-shaped branchial plate and their notochaetae are multiarticulated, at least in anterior or median chaetigers. The thick tunic is easily noticed although the sediment cover had not been adequately characterised either regarding its extension along the body or the type of sediment particles involved. At the same time, the type of neurochaetae has not been properly evaluated, and there have been some confusions regarding the different types present in the members of these genera. These factors have resulted in a problematic taxonomy which deserves to be improved.

The main feature to keep them separate relies on the type of neurochaetae, especially those found along posterior chaetigers. The first two genera have been revised elsewhere (Salazar-Vallejo 2011a); *Piromis* was restricted to include only species having multiarticulate bidentate neurohooks in median and posterior chaetigers, with articles medium-sized or long, whereas *Pycnoderma* was separated because its species are not provided with bidentate neurochaetae, but they are rather subdistally swollen, having entire or bifid tips, and few well-defined articles. In this contribution, *Trophoniella* is revised and redefined to include species having median or posterior neurochaetae with entire, bidentate or bifid tips, but whose articles are very short and anchylosed (barely defined).

MATERIAL & METHODS

The species are presented in alphabetical order but the type species comes first; some comments about photography are included below; for other details please refer to Salazar-Vallejo (2011a). Most morphological features follow the online polychaete glossary (Glasby *et al.* 2000).

Photographs were made with digital cameras, either a Sony Mavica or a Canon PowerShot G6, combined with the microscope and lamps available. Some specimens were immersed during 10-20 sec in a methyl-green, oversaturated, alcoholic solution, in order to improve the body surface contrast; this explains the greenish hue in some photos. Later, photos were edited using Photoshop pro 6 or 9 and, rarely, an automatic editing software was employed (HeliconFocus). The main problems stem from the chaetal fine details because the articulation pattern is better observed in the inner organisation, instead of the surface features, rendering the chaetal surface slightly off-focus, and this was problematic for editing the corresponding photos. The other problem was making photos of large specimens with a single lamp. This produced an illumination gradient which was difficult to solve and some photos show this, making them probably less visually attractive, but hopefully are clear enough for showing the body features.

On the other hand, from the 11 newly described species, two are based upon single specimens. This has been done once the morphological variation has been understood and with little hesitation, indeed, because their body attributes differ from those present in the most closely allied species, and they were found in different localities. Thus, they were named. These descriptions are expected to encourage the interest for doing further collections; hopefully, more specimens might become available in the near future to improve the included descriptions.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
BMNH	The Natural History Museum, London (formerly British Museum of Natural History);
CAS	California Academy of Sciences, San Francisco;
ECOSUR	Colección de Referencia, El Colegio de la Frontera Sur, Chetumal;
IRFA	Institut de Recherche fondamentale et appliquée, Université catholique de l'Orient, Angers;
LACM-AHF	Natural History Museum of Los Angeles County, Allan Hancock Foundation, Polychaete collection;
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge;

MNHN	Muséum national d'Histoire naturelle, Paris;
MUNHINA	Museo de Historia Natural y Antropología, Montevideo;
NTM	Museum and Art Gallery of the Northern Territory, Darwin;
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt;
SMNH	Swedish Museum of Natural History (formerly NHRM: Naturhistoriska Riksmuseet), Stockholm;
UANL	Laborarorio de Biosistemática, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Monterrey, Mexico;
UMML	Marine Invertebrates Museum, University of Miami, Rosenstiel School of Marine and Atmospheric Sciences, Miami;
USNM	National Museum of Natural History, Smithsonian Institution, Washington;
ZMA	Zoologisch Museum, Universiteit van Amsterdam, The Netherlands;
ZMB	Zoologisches Museum, Berlin;
ZMH	Zoologisches Museum und Institut, Universitat Hamburg, Hamburg;
ZMUC	Zoologisk Museum, København Universitet, Copenhagen.

RESULTS

MORPHOLOGY

Besides the morphological features explained elsewhere for two closely allied genera, *Piromis* and *Pycnoderma* (Salazar-Vallejo 2011a), the following features are especially useful for the species belonging to *Trophoniella.*

SEDIMENT COVER

The relative sediment cover and particle size are useful to separate similar species. On the basis of the distribution of sediment particles, three distinct patterns are recognisable: 1) dorsal and ventral surfaces, at least along the anterior region (Fig. 1A, B); 2) dorsal and sometimes lateral regions (Fig. 2A); and 3) without sediment (Fig. 11A, B). The latter would include those species having very few, sparse, sediment particles throughout the anterior region. Further, in those species deprived of sediment particles on the tunic, the body wall can be seen by transparency and its general colour could be used to separate similar species. However, it must be kept in mind that tunic transparency might vary during ontogeny, juvenile specimens being more transparent than older ones. This is explained by the ageing of the tunic surface, which might sometimes look like a wooly fibrous layer. This unusual appearance results from the thickening of the thin, proteinaceous cover along individual papillae, which might become thicker by the addition of very fine sediment particles, and is more easily seen if the animal tunic is contracted. The main result of this thickening is that it considerably reduces the tunic transparency. It is noteworthy that the sediment cover pattern is very stable and can be noticed even in some specimens retrieved from the stomach contents of demersal fishes (see below). Because of the presence of sediment particles on the chaetal emerging areas, they must be carefully removed before dissecting parapodia, because when parapodia are compressed by the forceps, they often fracture the chaetae. Thus, small incisions made transversally along chaetal emerging areas, and then the removal of parapodia by compression with the forceps would result in complete chaetal sets. However, if the removed portion is too thick, the excess of tunic and body wall muscles might be removed by additional cuts resulting in a flat portion and chaetal features would be easily observed in the compound microscope.

DORSAL TUBERCLES

In *Trophoniella* and *Piromis*, each segment has a basic pattern of two dorsal and four ventral, longer, sensory papillae. They are placed along the body at the same distance, forming longitudinal series and because the outer ones are closer to the chaetae, they have not been regarded as part of the same pattern, which might be better observed in juveniles. In those species carrying abundant sediment grains, only the papillae tips can be noticed and sometimes they are not visible at all, perphaps because they are fragile and easily eroded during sample sieving. On the contrary, in those species deprived of sediment particles, these papillae can be more easily noticed, if present. A few species have enlarged dorsal tubercles in anterior chaetigers, often larger in the more anterior segments and decreasing in size posteriorly (Figs 13B; 14A); they are formed by the dorsal papillae which are overgrown by a thicker cuticle. The number of chaetigers where these dorsal tubercles occur can be used to separate similar species.

NOTOCHAETAE

The number of notochaetae varies very little in a given species, 5-7 for example, along the body reaching its maximum in the wider, often median chaetigers. Thus, the number of notochaetae by chaetigers 10-11 is useful to separate similar species. The type of articulation is often regular and the articles can be separated by using the length/width proportions, resulting in short articles if they are wider than long, medium-sized if they are as long as wide, or long articles if they are longer than wide. The change in article length is progressive and the pattern is only rarely irregular, having one or two longer articles between shorter ones. When this pattern is present, it can be employed to separate similar species. It must be emphasised that the relative article length is defined as the proportion between length vs width and thus even if median and distal articles are of the same length, the distal ones will be regarded as longer because the chaeta becomes thinner.

NEUROCHAETAE

Trophoniella differs from both *Piromis* and *Pycnoderma* because the two latter genera have oligo- or multiarticulated neurochaetae, whereas in *Trophoniella* the neurochaetal articles in median or posterior chaetigers have become fused to each other, hence anchylosed (Salazar-Vallejo 2011a), and besides being short, the individual articles are often difficult to observe (Fig. 1E). When present, the first anchylosed neurohooks appear by replacing the lower and shorter chaetae in each bundle, such that they could be overlooked, and especially because they are less flexible, they might be more easily broken.

The neurochaetae can be separated into multiarticulated capillaries or hooks because the latter are thicker than the former, and because they usually have a smaller number of longer articles. Although there might be some size-dependent variation, the start of anchylosed neurohooks helps for separating species in the same genus, and although there might be subtile differences in the relative size of articles, the neurochaetae usually become shorter or markedly shorter after the first few chaetigers.

Thus, in *Trophoniella* species the anchylosed neurohooks can start very early along the body, replacing completely the multiarticulated neurohooks, or they can gradually replace them from median or posterior chaetigers. In any case, their first appearance is noteworthy and the starting point should be regarded as the first chaetiger wherein all or most neurochaetae are hooks of the same type, short and anchylosed. However, in some species, there are one or few transitional chaetigers carrying a combination of short and long neurochaetae and because they are fragile, the mixture might be difficult to detect. Then, it is recommended to carefully observe the neurochaetal bases because there will be differences in the relative length of the articles; anchylosed neurohooks have mostly short to very short fused articles or rings, and this will likewise help identifying the first neuropodia carrying the different type of neurochaetae, unless the fracture is such that the only chaetal remains are left within the tunic.

Anchylosed neurohooks have a more or less cylindrical basal region, often provided with very short anchylosed articles or rings, and often they can be extended up to the basal chaetal third or half. In several species, these anchylosed articles might reach the subdistal part of the hook; more rarely, they can continue almost to the chaetal tip. The median region is progressively compressed and often without any transverse articulation mark, but with fine to very fine oblique striae running through the median third of chaetae; this region can take three different patterns: 1) it can be straight, having parallel sides; 2) it can have convergent sides, or tapering; or 3) it might be laterally expanded. The tip has three different forms; it is generally entire and falcate (Figs 3E; 4H), or bidentate, with a larger tooth or fang, and an accessory tooth that is usually smaller than the fang (Figs 1E; 5E); the third form is only present in a single species, the neurochaetal tip is split into two sharp, similar projections, hence bifid (Fig. 24G). In bidentate neurohooks, the size relationship between fang and accessory tooth as well as the angle between the fang and the neurochaetal axis might be useful to separate similar species; however, because chaetal tips are often eroded, their use has not been overemphasised and is rather utilised below together with other morphological features. Further, because the accessory tooth is delicate, even foliose, and often broken off, several parapodia should be dissected and mounted before regarding their hooks as having entire tips.

SYSTEMATICS

Class POLYCHAETA Grube, 1850
Order FLABELLIGERIDA Pettibone, 1982
Family FLABELLIGERIDAE Saint-Joseph, 1894

Genus *Trophoniella* Hartman, 1959

Trophoniella Caullery, 1944: 35 (unavailable). — Fauchald 1977: 117.

Trophoniella Hartman, 1959: 423.

Therochaetella Hartman, 1967: 128. — Type species: *Therochaetella chilensis* Hartman, 1967, by original designation.

TYPE SPECIES. — *Trophoniella avicularia* Caullery, 1944, by original designation (Hartman 1959: 423).

DISTRIBUTION. — Species of the genus are found in tropical or subtropical regions, especially in sediments or mixed bottoms in shallow water (up to 200 m), but two species, *T. borealis* (Hartman, 1965) n. comb. and *T. hospita* (Fauchald, 1972) n. comb., were found in deeper water (500-600 m).

DIAGNOSIS. — Cephalic cage present. Tunic thick, mostly with sediment grains. Papillae arranged in longitudinal series, fragile, clavate, sometimes inconspicuous. Median chaetigers with multiarticulated or anchylosed neurochaetae, simple falcate or bidentate; posterior chaetigers with anchylosed neurochaetae, straight, tapering or subdistally expanded, tips entire, bidentate or bifid, never mucronate. Branchiae often abundant, short, cirriform filaments, on a tongue-shaped lobe; rarely, few filaments on a flat branchial plate.

REMARKS

The chronic confusion of the generic definitions deserves to be explained. Ehlers (1887: 158-161) identified some specimens as *Siphonostomum cariboum* Grube & Ørsted *in* Grube, 1859; he provided an extensive description and excellent illustrations for his specimens, which were followed by Saint-Joseph (1898: 367). Following Ehlers, Chamberlin (1919: 397) rightly proposed *Semiodera*, with *Siphonostomum cariboum* as its type species. However, the specimen that Ehlers illustrated differs from the holotype of *S. cariboum* (ZMUC 331), because this species has a well-developed dorsal shield over few anterior chaetigers, a very thin tunic, its body papillae are tiny without sediment cover, and its branchiae are few, arranged in 1-2 rows. Ehlers' specimen had few or no large sediment particles, but no dorsal shield, a very thick tunic, body papillae are long, especially in notochaetal lobes, the branchiae are abundant and arranged on a tongue-shaped plate, and neurochaetae are anchylosed. Consequently, his specimen belongs to an undescribed species of *Trophoniella*, which is described below as *T. lindae* n. sp.

The next confusion deals with *Trophoniella* Caullery, 1944. Caullery proposed this name ("n. nom. gen.", 1944: 35) to replace *Trophonia* Malmgren, 1867, that was introduced to replace *Pherusa* Oken, 1815, used before for other taxa. The type species for *Pherusa* is *Amphitrite plumosa* Müller, 1776, which had been proposed by Oken (1807) and confirmed by Støp-Bowitz (1948: 13). It must be emphasised that Caullery was following Malmgren's generic concept, which was based upon the corresponding concept by: "M. Edw. 1829 sec. Agassiz." But the original quote was: "Aud. et Edw. Litt. de la Fr. 1829 (Agassiz 1848: 1096)." It has been shown that this name was introduced elsewhere and is a *nomen nudum* (Salazar-Vallejo 2011b: 166). Further, Caullery indicated that his genus was not following Milne-Edwards (Caullery 1944: 35): "(= *Trophonia* Malmgren 1867, Levinsen 1883, LoBianco 1893, *nec* Audouin et Edwards 1829)". This is surprising because Malmgren (1867: 191) followed Milne-Edwards (1829), after Agassiz (1848); thus, Malmgren included two species in his proposed grouping, *Pherusa plumosa* (Müller, 1776) and *P. glauca* Malmgren, 1867, now called *Diplocirrus glaucus* (Malmgren, 1867). *Trophoniella* was apparently proposed for a junior homonym:

Trophonia Malmgren, 1867 vs *Trophonia* Milne-Edwards, 1836 (ICZN 1999: art. 60.3), and in so doing, they would become objective synonyms (ICZN 1999: art. 61.3.3 and art. 72.7). However, these generic concepts were addressed to different species or species groups. On the other hand, after ICZN (1999: art. 67.8), the type species for the original name and for the replacement name is the same, which would imply that *Trophoniella* Caullery, 1944 becomes a junior synonym of *Pherusa* Oken, 1807, which would result in a worse situation because the species content is very different. Consequently, *Trophonia* Malmgren, 1867 is regarded as a *nomen nudum* and *Trophoniella* is regarded as a new name.

Further, *Trophoniella* included three species after the original proposal, but the type species was not formally established and this would render the name unavailable (ICZN 1999: art. 13.3). However, this has been solved by a subsequent designation of the type species (ICZN 1999: art. 69.1). Hartman (1959: 423) recognised the genus as distinct and designated *T. avicularia* Caullery, 1944 as the type species; this was followed by Fauchald (1977: 117). This proposal made the name available and therefore it must be assigned to Hartman (ICZN 1999: art. 50.1).

Caullery (1944) indicated that: "*T. avicularia* rappelle *T. eruca* Clap. et *T. arenosa* Webster […] évidemment, il s'agit d'une espèce du même groupe, déjà distinguée par de Saint-Joseph." This would be translated as: "*T. avicularia* resembles *T. eruca* Clap. and *T. arenosa* Webster […] certainly, it is a species of the same group, already recognised as such by Saint-Joseph." Therefore, *Trophoniella* could be regarded as a close relative of *Piromis*, but there are some important differences in the neurochaetae between them and hence *Trophoniella* includes species having anchylosed neurochaetae with entire, bidentate or bifid tips. The two other species included in the genus, *T. intoshi* Caullery, 1944 and *T. sibogae* Caullery, 1944 do not belong to the genus because they have aristate neurochaetae; they should be transferred to *Brada* Stimpson, 1854. On the contrary, *Brada rigida* Caullery, 1944 that is provided with anchylosed neurochaetae should be transferred to *Trophoniella.* Likewise several other species currently included in different genera but having anchylosed neurohooks and branchial filaments in a tongue-shaped branchial plate are herein regarded as belonging in *Trophoniella* as well.

Fauchald (1977: 117) regarded *Semiodera* as a junior synonym of *Piromis*, perhaps by following Ehlers' description and illustrations, and stated that there were 10 species in the genus, all provided with a tongue-shaped branchial plate that could be entire or bifid, and uni- or bidentate neurohooks. However, Day (1973: 108) had redefined *Piromis* to include only those species provided with bidentate neurohooks, and he regarded those species with entire neurohooks as members of *Pherusa. Piromis arenosus* Kinberg, 1867, the type species for the genus, has bidentate neurohooks with long distal articles (Hartman 1949: 117, pl. 15, fig. 7), and a single tongue-like branchial plate (Day 1967: 664, fig. 32.4c). These features are diagnostic for species belonging to that genus as confirmed elsewhere (Salazar-Vallejo 2011a). Therefore, the species formerly included in *Piromis* because they have a tongue-like branchial plate, but are provided with neurohooks having very short, anchylosed articles in median or posterior chaetigers, should be transferred to *Trophoniella*, which must be redefined accordingly.

Therochaetella Hartman, 1967 (p. 128), which was proposed for *Therochaetella chilensis* Hartman, 1967 (p. 128), is a subjective junior synonym of *Trophoniella.* The paratypes (USNM 55551) include an undescribed species of *Bradabyssa* Hartman, 1967, which prompted the inclusion of an "elongated oral tube" as a diagnostic feature (Hartman 1967: 120, key), whereas the illustration letterings were transposed. The holotype, however, is a member of *Trophoniella*, with a low tongue-shaped branchial lobe. The presence of bidentate neurochaetae is stressed in the generic diagnosis for *Therochaetella* and in the type-species description, but the only illustration (pl. 37, fig. D, from chaetiger 25) depicts an unidentate hook. Further, the lettering of the figure was transposed; thus, what is indicated to be C should be D, and vice versa. Consequently, the species is herein restricted, redefined and transferred to *Trophoniella.*

Therefore, *Piromis* and *Trophoniella* share several features; both have tunics with variable amounts of sediment particles, especially over the dorsal surface, and longitudinal rows of elongated single papillae along the body. However, *Trophoniella* must be separated from *Piromis* on the basis of having differently constructed neurohooks, especially in posterior chaetigers; thus, whereas in *Piromis* they have at least one distal long article, that articulates with the previous one, in *Trophoniella*, as in some other flabelligerid genera, neurohooks have short or very short anchylosed articles, mostly fused to the next. This modification implies that some species must be transferred from elsewhere, including *Piromis*, to *Trophoniella.*

Within *Trophoniella*, besides the differences on the relative cover of sediment grains on the body wall, there are two different patterns on the start of anchylosed neurohooks. They might start before chaetiger 10, or they can start by chaetiger 15, but usually beyond it. The species having anchylosed or falcate neurohooks from anterior chaetigers are *T. americana* (Monro, 1928) n. comb. from Galápagos and Panama, *T. ehlersi* (Day, 1973) n. comb. from the eastern United States, *T. grandis* (Blanchard *in* Gay, 1849) n. comb. from central Chile, *T. havaica* (Kinberg, 1867) n. comb. from Hawaii, *T. incerta* (Augener, 1918) n. comb. from West Africa, *T. jareckiorum* n. sp. from the Caribbean Sea, *T. lindae* n. sp. from the Caribbean Sea, *T. minuta* (Blanchard *in* Gay, 1849) n. comb. from Chile, *T. reishi* n. sp. from the Gulf of California, *T. rigida* (Caullery, 1944) n. comb. from Indonesia, *T. rudis* (Grube & Müller *in* Grube, 1877) n. comb. from southern Brazil, *T. salazarae* n. sp. from western Mexico and *T. tumbensis* (Hartmann-Schröder, 1962) n. comb. from Chile.

All other species, including the type species, have anchylosed neurohooks beginning on more posterior chaetigers. These are *T. avicularia* Caullery, 1944 from Indonesia, *T. bastidai* n. sp. from western Mexico, *T. borealis* n. comb. from northeastern South America, *T. capitata* (Nonato, 1966) n. comb. from Brazil, *T. chilensis* (Hartman, 1967) n. comb. from Chile, *T. eliasi* n. sp. from central Argentina, *T. enigmatica* n. sp. from the Mediterranean Sea, *T. fauveli* n. sp. from the Mediterranean Egyptian coast, *T. fernandensis* (Augener, 1918) reinstated, n. comb. from northwestern Africa, *T. fiegei* n. sp. from the Persian Gulf, *T. harrisae* n. sp. from southern California, *T. hospita* n. comb. from the Gulf of California, *T. indica* (Fauvel, 1928) n. comb., n. stat. from the Bay of Bengal and *T. orensanzi* n. sp. from Uruguay.

KEY TO SPECIES OF THE GENUS *TROPHONIELLA* HARTMAN, 1959

1. Anchylosed neurohooks starting between chaetigers 4-7, continued throughout the body 2
— Anchylosed neurohooks starting from chaetiger 14, or from posterior chaetigers 15

2. Body with sediment particles 3
— Body almost without sediment particles, with very few, sparse sediment grains, or without sediment grains; anterior chaetigers sometimes with very few sediment particles, or with a thin, dark-brown or blackish crust 6

3. Sediment particles present over the dorsal and ventral surfaces 4
— Sediment particles concentrated dorsally, sometimes extending laterally 7

4. Sediment grains small, very abundant 5
— Sediment grains large; anterior chaetigers without dorsal tubercles or notopodial lobes; first neurohooks from chaetiger 5 9

5. Anterior chaetigers with dorsal tubercles but no notopodial lobes; first neurohooks from chaetiger 7 .... *T. grandis* (Blanchard *in* Gay, 1849) n. comb.
— Anterior chaetigers without dorsal tubercles or notopodial lobes; first neurohooks from chaetiger 5 .... *T. ehlersi* (Day, 1973) n. comb.

6. Neurohooks bifid; sediment particles mostly black .... *T. rigida* (Caullery, 1944) n. comb.
— Neurohooks entire; sediment particles mostly white .... *Trophoniella* sp. Brazil

7. Tunic with fine particles, difficult to be detected; notopodia with 6-7 chaetae per bundle; first neurohooks in chaetigers 5-6 .... *T. lindae* n. sp.
— Tunic with larger particles, easily noticed individually 8

8. Body wall pale or pinkish; few notochaetae (4-5) per bundle; anchylosed neurohooks from chaetigers 4-5 .... *T. americana* (Monro, 1928) n. comb.
— Body wall grayish; abundant notochaetae (8-10) per bundle; anchylosed neurohooks from chaetigers 5-7 .... *T. tumbensis* (Hartmann-Schröder, 1962) n. comb.

9. Some neurohooks bidentate; 7-9 notochaetae per bundle .... *T. incerta* (Augener, 1918) n. comb.
— All neurohooks entire, sometimes eroded 10

10. Body with few sediment particles over anterior chaetigers 11
— Body without sediment particles 12

11. Body dark pink, finely speckled with red spots, rarely pale; cephalic cage twice as long as body width; 6-8 notochaetae per bundle .... *T. reishi* n. sp.
— Body solid brown; cephalic cage 1.0-1.5 times as long as body width; 7-8 notochaetae per bundle .... *T. rudis* (Grube & Müller *in* Grube, 1877) n. comb.

12. Parapodial papillae digitate or slightly capitate; notochaetae with regular articulation 13
— Parapodial papillae markedly capitate (distally expanded); notochaetae with irregular articulation, several short articles followed by a medium-sized article, and then several short articles; with 5-6 notochaetae per bundle (body width 5 mm)............ *T. havaica* (Kinberg, 1867) n. comb.

13. Tunic smooth, transparent (at least in the anterior region); median chaetigers with about 10 notochaetae per bundle (body width 9 mm) .... *T. minuta* (Blanchard *in* Gay, 1849) n. comb.
— Tunic papillose, looking rugose or areolated, opaque or, if transparent, with fewer notochaetae 14

14. Tunic grayish to reddish, finely speckled with tiny black spots; 5-8 notochaetae per bundle (body width up to 10 mm), each with short articles basally, medium-sized medially, longer distally .... *T. salazarae* n. sp.
— Tunic whitish (transparent in juveniles), without any dark spots; 4-5 notochaetae per bundle (body width 3 mm), each with long articles only .... *T. jareckiorum* n. sp.

15. Tunic with sediment grains on dorsal and ventral surfaces 16
— Tunic without sediment grains 25

16. Sediment grains large, completely covering the tunic 17
— Sediment grains variable, often small; if large, often embedded in the tunic, without concealing it 20

17. Sediment particles completely immersed in the tunic; first short neurohooks from chaetiger 5; anchylosed neurohooks bidentate, slightly expanded subdistally, from chaetiger 25 .... *T. chilensis* (Hartman, 1967) n. comb.
— Sediment particles partially immersed in the tunic 18

18. Anterior chaetigers with dorsal tubercles 19
— Anterior chaetigers without dorsal tubercles; anchylosed neurohooks from chaetigers 18-20; neurohooks with accessory tooth about as long as fang ..... *T. avicularia* Caullery, 1944

19. Anchylosed neurohooks from chaetiger 14; neurohooks with accessory tooth longer than fang .... *T. indica* (Fauvel, 1928) n. comb., n. stat.
— Anchylosed neurohooks from chaetiger 40; neurohooks with accessory tooth about as long as fang .... *T. enigmatica* n. sp.

20. Sediment particles often small, completely covering the tunic or dispersed throughout it 21
— Sediment particles larger, dispersed throughout the tunic 24

21. Anterior chaetigers with both notopodial and dorsal tubercles 22
— Anterior chaetigers with notopodial tubercles; dorsal tubercles absent .... *T. eliasi* n. sp.

22. Dorsal tubercles extending through a short anterior region, up to chaetiger 10 (body 5 mm wide); anchylosed neurohooks from chaetiger 32 .... *T. orensanzi* n. sp.
— Dorsal tubercles extending through a larger anterior, over at least 20 chaetigers 23

23. Anchylosed neurohooks from chaetiger 25; dorsal tubercles extending up to chaetiger 25 (body 5 mm wide) .... *T. hospita* (Fauchald, 1972) n. comb.
— Anchylosed neurohooks from chaetiger 20; dorsal tubercles extending up to about chaetiger 40 (body 10 mm wide) .... *T. harrisae* n. sp.

24. Anterior chaetigers with notopodial lobes, without dorsal tubercles; first short neurohooks from chaetiger 10; anchylosed neurohooks from chaetiger 40 .... *T. fauveli* n. sp.
— Anterior chaetigers without notopodial or dorsal tubercles; first short neurohooks from chaetiger 5; anchylosed neurohooks from chaetiger 28 .... *T. capitata* (Nonato, 1966) n. comb.

25. Tunic smooth, papillae barely visible dorsally, median chaetigers almost without emerging papillae; anterior chaetigers with notopodial tubercles 26
— Tunic papillose or velvety, not smooth 27

26. Chaetigers 2-5 with large notopodial lobes, larger in chaetigers 3-5; all neurohooks anchylosed from chaetiger 26; 6-7 notochaetae per bundle .... *T. bastidai* n. sp.
— Chaetigers 2-3 with large notopodial lobes, not visible in other anterior chaetigers; all anchylosed neurohooks from chaetiger 32; 7-8 notochaetae per bundle .... *T. borealis* (Hartman, 1965) n. comb.

27. Median chaetigers with 6-9 transversal rows of papillae per segment; anchylosed neurochaetae slightly expanded medially, starting from chaetiger 50; tunic appearing smooth .... *T. fiegei* n. sp.
— Median chaetigers with about 15 transversal rows of papillae per segment; anchylosed neurohooks markedly medially expanded, starting from chaetiger 45; tunic velvety or rugose .... *T. fernandensis* (Augener, 1918) reinstated, n. comb.

Trophoniella avicularia Caullery, 1944
(Fig. 1)

Trophoniella avicularia Caullery, 1944: 35, 36, fig. 27. — Bleeker & Van der Spoel 1992: 163.

Pherusa eruca indica – Al-Hakim & Glasby 2004: 38 (*non* Fauvel 1928).

TYPE MATERIAL. — **Indonesia**. Holotype of *Trophoniella avicularia* (ZMA 1598), Irian Jaya, R/V *Siboga* expedition, stn 162, between Loslos and Broken Island, Salawatti, W coast, 18 m, dredge, sand, shells, 18.VIII.1899.

ADDITIONAL MATERIAL. — **Indonesia**. 1 specimen (ZMB 123) damaged, in 2 pieces, stn NB20B (03°34.92'N, 107°58.54'E), off Natuna Barat, 105 m, 3.VIII.2001, I. Al-Hakim (32 (19 + 13) mm long, 2.5 mm wide, cephalic cage 2.5 mm long, 79 (38 + 41) chaetigers).

DISTRIBUTION. — Only known from two localities in Indonesia, from shallow water to 105 m depth.

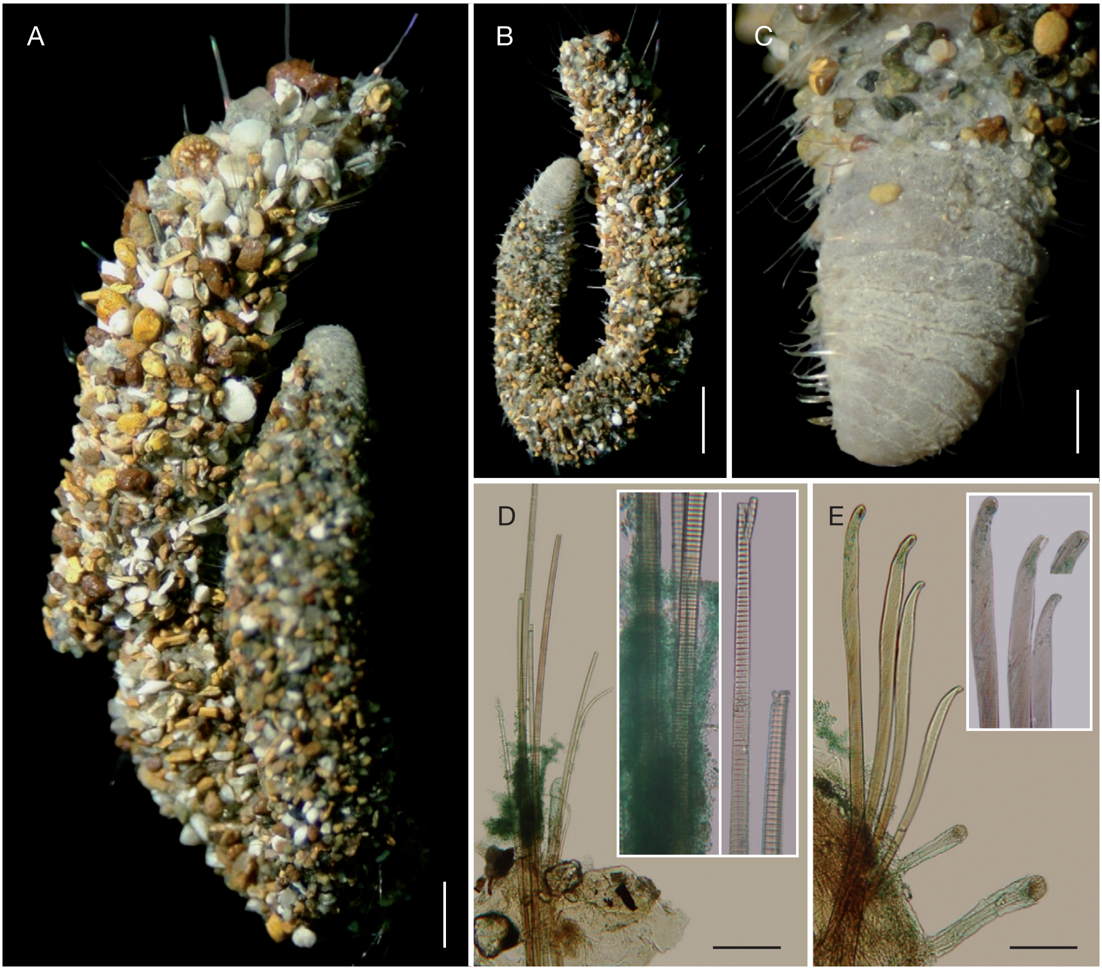

Fig. 1. — *Trophoniella avicularia* Caullery, 1944, holotype (ZMA 1598): **A**, dorsal view; **B**, ventral view; **C**, posterior end, ventral view; **D**, chaetiger 17, notopodium (insert: basal and medio/subdistal notochaetal regions); **E**, chaetiger 34, neurohooks (insert: tips of basal three hooks). Scale bars: A, 1.2 mm; B, 2.3 mm; C, 0.33 mm; D, 200 µm; E, 115 µm.

DESCRIPTION

Holotype (ZMA 1598) complete. Tunic thick, heavily covered by sand, shell fragments, forams and other large particles dorsally and ventrally (Fig. 1A, B); posterior end grayish, without sediment cover (Fig. 1C). Body cylindrical, tapering posteriorly, 29 mm long, 3.5 mm wide, cephalic cage 5 mm long, 49 chaetigers. Body papillae long, capitate, sparse, arranged in longitudinal rows, five dorsally, three ventrally; difficult to follow because of the size of foreign particles.

Anterior end not observed; holotype not dissected. Cephalic cage damaged, chaetae as long as ⅙ body length or 1.3 times longer than body width. Chaetigers 1-3 involved in the cephalic cage; chaetae of chaetiger 1 arranged in short dorsal and ventral series; others in short ventrolateral series. Chaetiger 1 with two chaetae per bundle, one neurochaeta thicker; chaetiger 2 with two chaetae per bundle, neurochaetae of about the same thickness; chaetiger 3 with three chaetae per bundle.

Anterior dorsal margin of first chaetiger papillated, without projection. Anterior chaetigers without especially long papillae. Chaetigers 1-3 enlarging posteriorly. Chaetal transition from cephalic cage to body chaetae gradual; anchylosed, bidentate neurohooks starting by chaetiger 18. Gonopodial lobes not seen.

Parapodia poorly developed (Fig. 1D, E); chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia short lobes with 4-6 papillae per bundle. Noto- and neuropodia distant to each other.

Median notochaetae arranged in short longitudinal series, about 6-8 (3-5 remains) per bundle, as long as ⅓ body width; all notochaetae multiarticulated capillaries, articles short throughout the chaetae (Fig. 1D, insert), slightly longer near the tip, tips falcate, most broken. Neurochaetae multiarticulated neurohooks in chaetigers 1-17; each straight, with short articles, becoming slightly longer near the falcate tip; by chaetiger 15, smaller hooks together with multiarticulated falcate capillaries. By chaetiger 20, all neurohooks anchylosed, curved distally, darker, medially widened, subdistally expanded, with short rings continued to the subdistal hyaline region, tip bidentate, accessory tooth wide, not passing fang (Fig. 1E, insert); neurohooks arranged in transverse series, 4-5 per bundle.

Posterior end (Fig. 1C) mostly without sediment (last nine chaetigers at least), tapering to a blunt cone; pygidium with anus terminal; no anal cirri.

REMARKS

Caullery (1944) overlooked the first chaetiger when he described *T. avicularia*, because of its very small size and because chaetae were broken. As stated above, he thought his species was clearly associated with *T. eruca* Claparède, 1868 because both have bidentate neurohooks. He overlooked Fauvel (1928: 7), who had provided a short description and illustrations for his *S. eruca indica* Fauvel, 1928, noticing that his new variety was closely allied to *Stylarioides eruca* but differing in having longer, thinner neurochaetae. This implies that Fauvel noticed that parapodial lobes are pointed and directed forwards, as it is the case in the supposedly parental form. However, their neurochaetae are markedly different because they have anchylosed, short articles restricted to the base or up to the median chaetal region, and hooks can be distally expanded, hyaline, whereas in *Piromis* the neurohooks are multiarticulated, having longer articles, rarely distally expanded, and rings are visible up to the subdistal chaetal region.

Trophoniella avicularia is closely allied to *T. indica* n. comb., n. stat. (see below), but they differ in the relative development of the notopodial lobes in anterior chaetigers, and in the distal chaetal article. In *T. avicularia*, the notopodial lobes are reduced, not forming any prominent lobe, whereas in *T. indica* n. comb., n. stat. they are well delineated and pointing forward. Further, the bidentate neurohooks have different proportions in teeth size; in *T. avicularia* the accessory tooth is short, never passing the fang, whereas in *T. indica* n. comb., n. stat. they are larger, often passing the fang. The other specimen (ZMB 123) is regarded as belonging to the same species with hesitation, because the neurohooks are straight and subdistally swollen, but because it is damaged, its recognition as a distinct, separate species should be postponed.

Trophoniella americana (Monro, 1928) n. comb.
(Fig. 2)

Stylarioides capensis americana Monro, 1928: 96, 97, fig. 16; 1933: 1057, 1058, textfig. 6 *partim*.

Piromis americana – Hartman 1961: 123. — Fauchald 1972: 415 *partim*.

Semiodera glabra Treadwell, 1928: 479, 480, fig. 179: 62-65.

TYPE MATERIAL. — **Eastern tropical Pacific**. Lectotype of *Stylarioides capensis americana* (BMNH 1933.7.10.144), by present designation, cut in 2 pieces, anterior fragment ventrally dissected, labeled "Balboa, Galapagos", C. Crossland; 4 paralectotypes of *S. c. americana* (BMNH 1933.7.10.138/9), damaged, 1 broken in 2 pieces, off Balboa, Panama, 1923/4, C. Crossland (19.0-24.5 mm long, 1.5-2.5 mm wide, cephalic cage 3-4 mm long, 44-56 chaetigers, first neurohooks from chaetiger 5).
Holotype and 2 paratypes of *Semiodera glabra* (AMNH 3520), 1 complete paratype, off Isla Española (01°22'59"S, 89°39'00"W), Galápagos Islands, 5 m, 25.IV.1925 (holotype 24 mm long, 4.0 mm wide, cephalic cage 4.5 mm long, 49 chaetigers; larger paratype 7 mm long, 1.2 mm wide, cephalic cage 2.0 mm long, 40 chaetigers).

ADDITIONAL MATERIAL. — **Eastern tropical Pacific, Gulf of California**. 1 specimen (LACM-AHF 2484), E of La Paz, Baja California Sur, 21.III.1940, E. Ricketts (37 mm long, 4 mm wide, cephalic cage 5 mm long, 54 chaetigers). — 1 specimen (ECOSUR), among mussel beds, Bahía de Los Angeles, Baja California, 2 m depth, 27.III.1985, E. & C. Aguirre (16 mm long, 3.5 mm wide, cephalic cage 4 mm long, 55 chaetigers). — 1 specimen (ECOSUR), Playa El Caimancito, La Paz, Baja California Sur, mixed bottom (rocks and sand), 1 m depth, 8.X.1987, J. A. de León & S. I. Salazar-Vallejo (33 mm long, 5 mm wide, cephalic cage 5.5 mm long, 60 chaetigers).
Western Mexico. 1 specimen (ECOSUR), Islas Marietas, Nayarit, mixed bottom (rocks and sand), 1 m depth, 27.XI.2004, P. Salazar & B. Yáñez (6 mm long, 2 mm wide, cephalic cage 2.5 mm long, 48 chaetigers). — 1 specimen (ECOSUR), Sayulita, Nayarit, mixed bottom, intertidal, 28.XI.2004, P. Salazar & B. Yáñez (54 mm long, 4 mm wide, cephalic cage 5 mm long, 91 chaetigers). — 1 specimen (ECOSUR), Playa Manzanilla, Nayarit, mixed bottom (rocks and sand), 1 m depth, 29.XI.2004, P. Salazar & B. Yáñez (19 mm long, 3 mm wide, cephalic cage 4.5 mm long, 59 chaetigers). — 1 specimen (ECOSUR), broken in 2, Muelle Balleto, Islas Marías, Nayarit, mixed bottom (rocks and sand), 1 m depth, 2.XI.1979, S. I. Salazar-Vallejo (13 mm long, 2 mm wide, cephalic cage 3 mm long, 55 chaetigers).
Panama. 6 specimens (ECOSUR), juveniles, Club de Yates, 1.VI.2002, L. Harris & S. I. Salazar-Vallejo (4-9 mm long, 1.0-1.5 mm wide, cephalic cage 1.5-3.0 mm long, 32-49 chaetigers; first neurohooks in chaetiger 5; very few sediment particles). — 2 specimens (USNM 66368), partially dried-out, Paitilla Beach, 28.X.1970, A. A. Reimer.
Ecuador. 2 specimens (LACM-AHF 2485), a mature ♀ and a small juvenile with sediment grains dorsally, Manta Bay, R/V *Velero III*, stn 400 (00°56'30"S, 80°44'18"W), shore, rock and sand, 19.I.1935 (♀, incomplete posteriorly, 55 mm long, 4.5 mm wide, cephalic cage 5 mm long, 69 chaetigers; oocytes 100 µm in diameter; juvenile 9 mm long, 1.5 mm wide, cephalic cage 1.5 mm, 39 chaetigers; dorsal and chaetal lobes papillae larger than in adults). — 1 specimen (USNM 1132100) apparently fixed in alcohol, Salinas, no further data, 12.IX.1926 (40 mm long, 5.5 mm wide, cephalic cage 5 mm long, 60 chaetigers; regenerating the last 20 chaetigers).

LECTOTYPE LOCALITY. — The lectotype has a label indicating "Balboa, Galápagos". This label is confusing because "Balboa" is on the Panamian Pacific coast whereas "Galápagos" indicates the archipelago, but because the species distribution includes both localities, no restriction is needed nor easy to discern.

DISTRIBUTION. — Gulf of California to Ecuador and the Galápagos Islands, in shallow subtidal depths. The records in California (Hartman 1969: 305) are questionable.

DESCRIPTION

Lectotype of *S. c. americana* (BMNH 1933.7.10.144), cut in 2 pieces (Fig. 2A), anterior fragment ventrally dissected. Body cylindrical, posteriorly tapered, body wall pinkish or pale, 77 mm long, 5.5 mm wide, cephalic cage 9 mm long, 93 chaetigers. Tunic thick, papillated, with sediment grains dorsally, extending laterally; ventral papillae tiny, abundant, larger papillae in longitudinal rows, three dorsally, four ventrally.

Cephalic hood exposed in holotype, short, margin smooth (Fig. 2B). Prostomium low cone, eyes faded; caruncle well developed, separating the branchial plate in two halves. Palps lost, palp keels low, rounded. Branchiae cirriform, sessile on a tongue-like protuberance; arranged in three rows per side, with many filaments each; branchial plate distally fused in juveniles. Lectotype (BMNH 1933.7.10.144) with distally notched branchial plate (Fig. 2C); most filaments lost; size relationship with palps unknown.

Cephalic cage chaetae as long as 1/9 body length, about twice as long as body width (larger or smaller specimens). Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short series, each about the body corners in the smaller syntype, dorsolateral in the larger one, 2-3 noto- and 4-5 neurochaetae.

Anterior dorsal margin of first chaetiger with a papillated margin, partially damaged; chaetigers 1-4 with long notopodial papillae. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt. Chaetiger 4 with transitional neurohooks; falcate anchylosed neurohooks from chaetiger 5. Gonopodial lobes in chaetiger 5, small, yellowish (lacking in the smaller syntype, no paralectotype).

Parapodia better developed in chaetigers 1-4, posterior ones less developed, placed over the body corners. Median neuropodia ventrolateral. Notopodia as a short conical lobe, one short and one long postchaetal papillae, becoming longer in posterior chaetigers. Neuropodia flat transversal lobe, with two longer papillae, one superior, and one postchaetal (Fig. 2D).

Median notochaetae arranged in longitudinal short series, 4-5 per bundle, as long as ⅓ body width; all multiarticulated capillaries, articles short basally, medium-sized to long medially, long distally (Fig. 2E). Smaller paralectotype with neurochaetae multiarticulated capillaries in chaetiger 1, chaetigers 2-4 with transition hooks, each with falcate tips, becoming shorter, distally widened. Anchylosed neurohooks entire, from chaetiger 5, arranged in transverse series, 3-4 anteriorly, 5-6 medially (Fig. 2F), 2-4 posteriorly, thinner, each subdistally straight, with a subdistal oblique dark spot, short articles feebly developed, continued to the median region.

Posterior end short, conical, with long papillae; pygidium with anus terminal, no anal cirri.

REMARKS

Trophoniella americana n. comb. is a senior synonym of *T. glabra* (Treadwell, 1928). The former was published on 28 July 1928, as indicated in the reprint's last page, whereas the second was published on 5 December 1928 (Steve Johnson pers. comm.). The printed number code was not easily identified as the publication date, until several volumes of the same journal became available online; the number code was then confirmed as the publication date. Before that the priority was not settled and some specimens identified as *T. glabra* should be relabeled as *T. americana* n. comb.

Monro (1928) described *Stylarioides capensis americana* using several specimens collected in both Pacific Panama and Galápagos, whereas Treadwell (1928) described *Semiodera glabra* from Isla Española, Galápagos Islands and Ecuador. However, this latter name was not used again, mainly due to a confusion about the type locality that Treadwell had indicated; thus, he stated as the type locality the coordinates for one island in Galápagos (Treadwell 1928: 480), but in a later paper, he stated the type material was coming from Haiti (Treadwell 1929: 9; Hartman 1956: 294), and that it was identical with *Stylarioides dubius* Treadwell, 1929. The confusion stems from the similarity between the two Spanish names: Isla Española, also known as Hood Island in Galápagos, and Hispaniola, the island now separated into Haiti and the Dominican Republic.

On the other hand, Monro (1928: 97) proposed *Stylarioides capensis americana* because he did not find any "trace in the dorsal chaetae of the small terminal hook described by both McIntosh and Gravier". He later redefined the new variety, after finding the falcate notochaetae, and then he diagnosed it (Monro 1933: 1058) by "the absence of the bold, transverse, distal striae [= articulation] on the ventral hooks […] described and figured by McIntosh" and by having neurospines from chaetigers 6-7. Further, Monro (1933: 1057, 1058) restricted the definition of his new variety by using two basic features: the lack of striae (articles) in neurospines, which defines *Piromis capensis* (McIntosh, 1885), which is in turn a junior synonym of *P. arenosus* Kinberg, 1867, and the start of neurospines by chaetigers 6-7. His syntypes, albeit damaged, have anchylosed neurospines (starting in chaetiger 5), such that they cannot fit *Piromis* but rather belong into *Trophoniella*, as proposed here.

Treadwell (1928: 479) indicated that "the type which is more than twice as large as any other in the collection is 30 mm long". All the specimens were together in the same vial, but this does not invalidate regarding one of them as the holotype (ICZN 1999: art. 73.1.1). Further, there are other materials which could have been regarded as paratypes; they were not examined because Treadwell stated that they were even smaller. Concerning the suspected synonymy with *Stylarioides dubius*, as stated by Treadwell, it has to be rejected; *S. dubius* is provided with a dorsal shield, has a very thin tunic and short papillae in transverse rows. Hence, it belongs in *Semiodera*, as will be shown in a forthcoming contribution. Hartman (1956: 294, 295) noticed the change in the type locality mentioned above, indicating that it could be the same as *S. cariboum*, and that it could also include *S. c. americana.* In fact, Monro included different forms under the same name and some former syntypes have been subsequently separated as members of other species (see below), whereas his name has been restricted to those forms with sediment particles over the dorsal and lateral surfaces, and having anchylosed neurohooks from early chaetigers (5-7).

Trophoniella americana n. comb. is closely allied to *T. tumbensis* n. comb. because their tunics have large sediment particles over the dorsal surface and often extending laterally. They differ in two main features; *T. americana* n. comb. has fewer notochaetae (3-5) than *T. tumbensis* n. comb. (8-10), and its

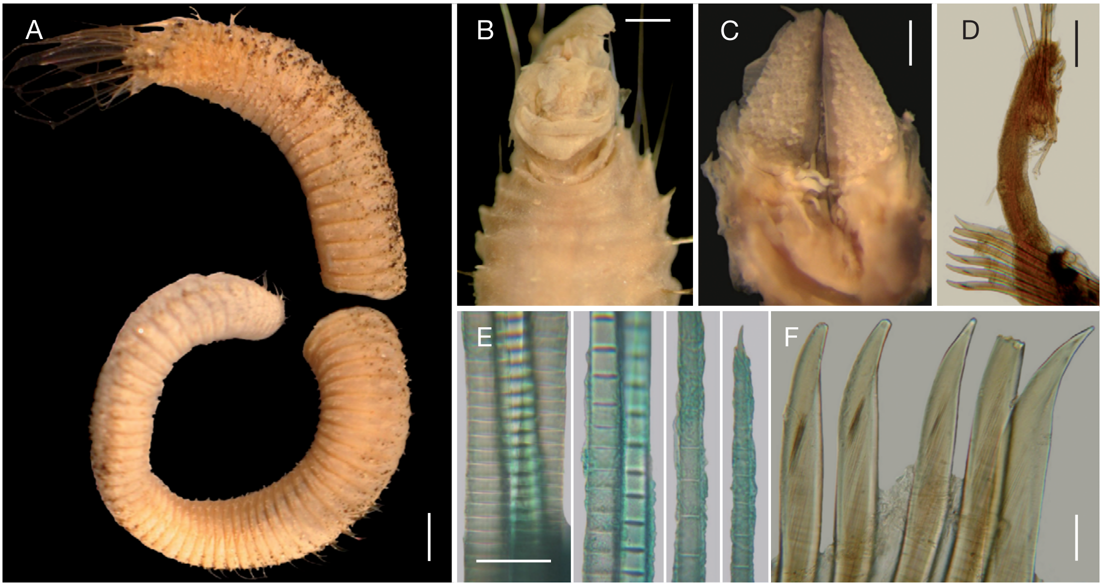

FIG. 2. — *Trophoniella americana* (Monro, 1928) n. comb.: **A**, syntype of *Stylarioides capensis americana* Monro, 1928 (BMNH 1933.7.10.144), lateral view; **B**, holotype of *Semiodera glabra* Treadwell, 1928 (AMNH 3520), anterior end, frontal view; **C**, syntype of *S. c. americana* (BMNH 1933.7.10.144), anterior end, dissected; **D**, holotype of *S. glabra*, parapodium from chaetiger 13; **E**, same, notochaetal basal, medial and distal regions; **F**, same, neurohooks. Scale bars: A, 2.5 mm; B, 0.7 mm; C, 0.22 mm; D, 0.15 mm; E, 40 µm; F, 30 µm.

body wall is pale or pinkisk whereas it is grayish in *T. tumbensis* n. comb.

The syntypes include some specimens that belong to *T. grandis* n. comb., and therefore, in order to clarify the delineation for the species, one lectotype has been selected from the type series (ICZN 1999: art. 74).

Trophoniella bastidai n. sp.
(Fig. 3)

Piromis gracilis – Hartman 1961: 123, 124, pl. 29, figs 1-4, pl. 30, figs 1-9 *partim*.

TYPE MATERIAL. — **Eastern tropical Pacific.** Holotype (LACM-AHF 2481), broken in 2 pieces, most chaetae broken, Chacahua Bay, Mexico, R/V *Velero III*, stn 767 (15°55'00"N, 97°41'00"W), 5.5 km S off Chacahua Lagoon mouth, mud, 40-50 fathoms, 9.I.1938.

TYPE LOCALITY. — Chacahua Bay, 5.5 km S of Chacahua Lagoon mouth, in 80-100 m depth.

DISTRIBUTION. — Restricted to the type locality, Chacahua Bay, Oaxaca, Mexican Pacific coast, in 80-100 m depth.

ETYMOLOGY. — This species is being named after my friend and colleague Dr J. Rolando Bastida-Zavala, as a means of appreciation and recognition of his work leading a group of polychaetologists in the Universidad del Mar, Oaxaca. Because the species was found in that Mexican state, it might promote their interest in finding more undescribed species.

DESCRIPTION

Holotype (LACM-AHF 2481), broken in two pieces, matching together, without posterior end (Fig. 3A), pale brown, slightly reddish-brown anteriorly. Tunic without sediment grains, smooth, transparent dorsally, pale, rugose ventrally.

Body club-shaped, wider anteriorly, tapering posteriorly, 84 (44 + 40) mm long, 8 mm wide, cephalic cage 17 mm long, 52 (25 + 27) chaetigers. Body papillae mostly eroded, few remaining in chaetal lobes and body depressions, more visible in posterior region; papillae darker than body wall; dorsal papillae arranged in four longitudinal series as two dorsolateral pairs; ventral papillae arranged in two longitudinal, ventrolateral series.

Anterior end not exposed; not dissected to avoid further damage. Branchiae cirriform, slightly everted (Fig. 3C). Cephalic cage chaetae about as long as 1/6 body length, twice as long as body width. Chaetigers 1-2 involved in the cephalic cage (Fig. 3B), chaetiger 3 with long chaetae, not reaching the longer chaetae of preceding chaetigers; chaetae arranged in short dorso- and ventrolateral series, 16-18 noto- and 14-16 neurochaetae in chaetiger 1, and 14-16 noto- and 12-14 neurochaetae in chaetiger 2. Anterior dorsal margin of first chaetiger eroded, probably with a lobe; body wall dark, exposed, two short lateral papillae remain. Anterior chaetigers with notopodial tubercles and a postchaetal row of capitate, long papillae in neuropodia (Fig. 3B).

Chaetiger 1 slightly shorter than chaetigers 2-3. Notopodial lobes globose in chaetigers 2-9, larger in chaetigers 3-5, shorter afterwards, visible to chaetiger 23. Chaetal transition from cephalic cage to body chaetae gradual; falcate anchylosed neurohooks starting by chaetiger 26, apparently all multiarticulate chaetae being replaced at the same time. Gonopodial lobes not visible.

Parapodia better developed in anterior chaetigers, placed on the body corners. Median neuropodia ventrolateral. Notopodia long, lobate, with 4-6 cirriform, capitate, postchaetal papillae. Neuropodia lobes long, with 4-6 cirriform, capitate, postchaetal papillae.

Median notochaetae arranged in short, oblique series, 6-7 per bundle, as long as ⅕ body width; all notochaetae multiarticulated capillaries, short articles basally and medially (Fig. 3D), slightly longer distally. Neurochaetae multiarticulated capillaries in chaetigers 1-25, but only distal part clearly articulated, most part of chaetae anchylosed; by chaetiger 26, all neurochaetae falcate, anchylosed, tips pale. Neurochaetae arranged in transverse series in median chaetigers, becoming oblique in posterior chaetigers, 4-6 in median chaetigers, 5 in posterior chaetigers, each subdistally tapering to a blunt (broken) tip (Fig. 3E), short articles present to the subdistal region.

Posterior end unknown.

REMARKS

Trophoniella bastidai n. sp. is closely allied to *T. borealis* n. comb. (see below). These species include large specimens with an almost smooth tunic, with notopodial lobes in some anterior chaetigers and by having anchylosed neurohooks from median or posterior chaetigers. They differ by the number of chaetae of the cephalic cage, 14-18 per bundle, in *T. bastidai* n. sp., against 5-7 in *T. borealis* n. comb.; also, *T. bastidai* n. sp. has larger notopodial lobes, extending through the first 10 chaetigers, whereas they are restricted to the first few chaetigers in *T. borealis* n. comb.The holotype of *T. bastidai* n. sp. was included as part of the type series of *Piromis gracilis*, which is now regarded as a member of *Pycnoderma* Grube, 1877 (Salazar-Vallejo 2011a: 41). The combination of a tunic without sediment cover, the presence of notopodial lobes, and the posterior start of falcate, anchylosed neurohooks indicates that it deserves an independent specific status.

Trophoniella borealis
(Hartman, 1965) n. comb.
(Fig. 4)

Buskiella borealis Hartman, 1965: 174-176, pl. 36, figs a-f.

TYPE MATERIAL. — **Central western Atlantic**. Holotype of *Buskiella borealis* (LACM-AHF 544) and 6 paratypes (LACM-AHF 545), N off Amazon River mouth, R/V *Chain*, stn Ch. 35 Dr. 33 (07°52'N, 54°31.5'W → 07°55'N, 55°35'W), 520-550 m, 25.IV.1963. H. Sanders (paratypes 1 complete, 5 incomplete, with darker anterior end, posterior end pale; complete 73 mm long, 5 mm wide, cephalic cage 8 mm long, 43 chaetigers; incomplete 54-142 mm long, 5-8 mm wide, cephalic cage 8-18 mm long, 30-51 chaetigers; additional anterior fragments 85-147 mm long, 5-8 mm wide, 27-53 chaetigers, gonopodial papillae not seen).

ADDITIONAL MATERIALS. — **Central western Atlantic.** 4 anterior fragments (USNM 1132098), off French Guiana, R/V *Oregon*, cruise 13, stn 10823 (07°40'N, 53°53'W), 300 fathoms, 27.XI.1969. — 1 complete and an anterior fragment (MCZ 32480), Guiana Basin, R/V *Knorr 25*, stn 296 (07°44.5'N, 54°19.1'W), 499-508 m, 28.II.1972 (complete 126 mm long, 6 mm wide, cephalic cage 16 mm long, 57 chaetigers; rows of papillae, undamaged, in posterior region).
Caribbean Sea. 2 specimens (ECOSUR, UMML), without posterior end, most chaetae broken, University of Miami Deep Sea expeditions, R/V *Pillsbury*, stn 781 (11°30'N, 73°26'W), off between Cabo de la Aguja and Riohacha, Colombia, 549 m, mud and pteropod shells,

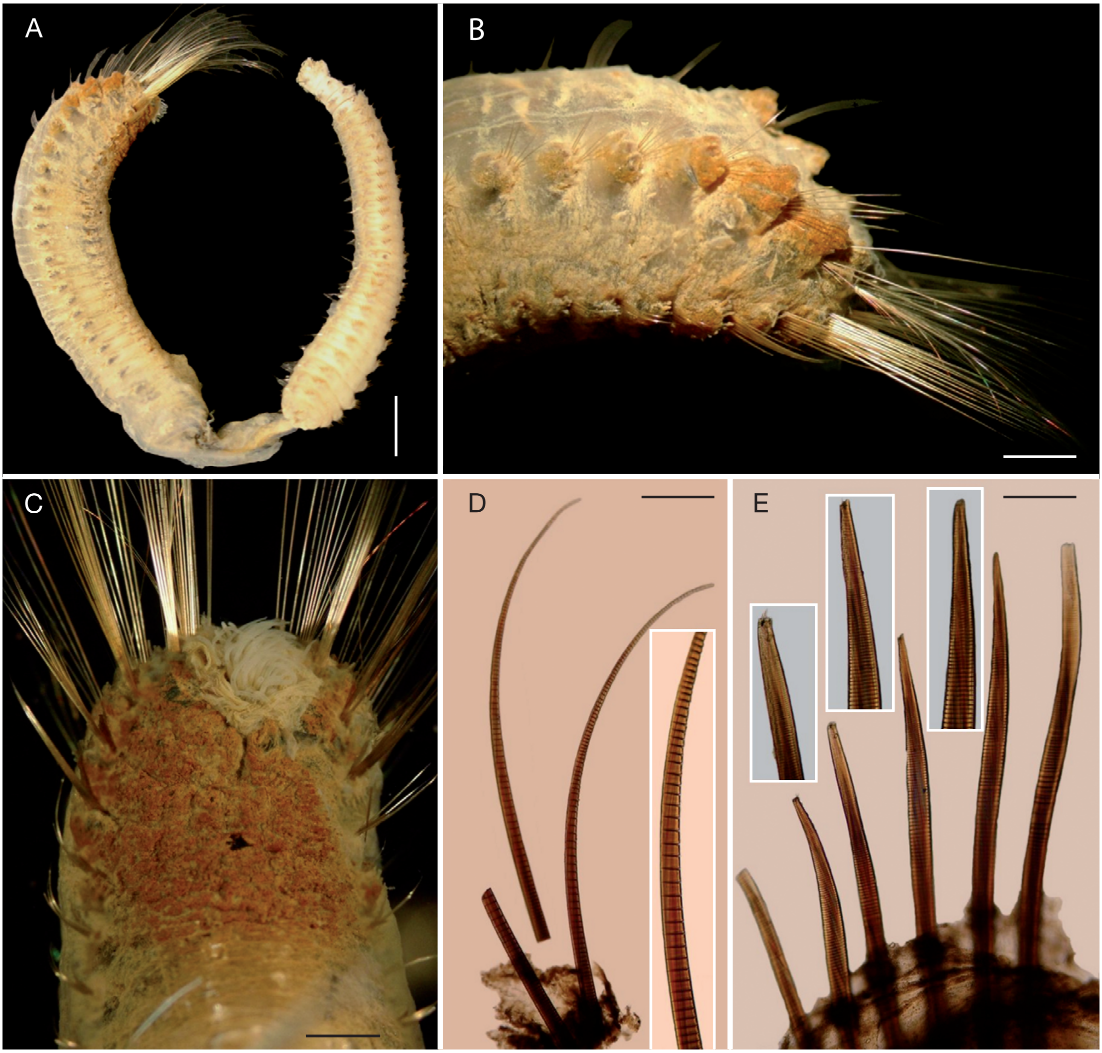

FIG. 3. — *Trophoniella bastidai* n. sp., holotype (LACM-AHF 2481): **A**, lateral view; **B**, anterior end, lateral view; **C**, anterior end, ventral view; **D**, chaetiger 11, notochaetae (insert: basal and medial notochaetal regions); **E**, chaetiger 31, neurochaetae (inserts: neurochaetal broken tips). Scale bars: A, 6.7 mm; B, 2.6 mm; C, 1.6 mm; D, 185 µm; E, 270 µm.

30.VII.1968 (67-81 mm long, 5-6 mm wide, cephalic cage broken, 35-38 chaetigers).

DISTRIBUTION. — From Colombia to northern Brazil, in sediments at 499-600 m depth.

DESCRIPTION

Holotype (LACM-AHF 544) without posterior end, first three chaetigers previously removed (placed in a separate vial), pale yellowish, darker anteriorly (Fig. 4A). Tunic mostly smooth, transparent, thick, tough, finely granulose, almost no sediment particles (Fig. 4C, D). Body cylindrical, slightly tapered posteriorly, 145 mm long, 7 mm wide, cephalic cage 17 mm long, 57 chaetigers. Body papillae thin, filiform, distally capitate, smothered in exposed surfaces, visible in depressions and in some posterior chaetigers, arranged in two longitudinal series dorsally and in four longitudinal series ventrally; other long papillae placed in noto- and neurochaetal lobes.

Cephalic hood exposed, short, margin finely papillated. Prostomium low, without eyes; caruncle well developed, dissects branchial lobe. Palps large, corrugated in holotype (Fig. 4B); palp keels low, rounded. Branchiae cirriform, sessile on a short tongue-like protuberance, about 25 filaments per side (Fig. 4F); some branchiae as long as palps, other shorter (one pair of nephridial lobes visible on the base of branchial plate in non-type specimen USNM 1132098).

Cephalic cage chaetae about as long as $\frac{1}{10}$ body length, almost twice as long as body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short dorso- and ventrolateral series, 6-7 noto- and 5-6 neurochaetae per chaetiger. Anterior dorsal margin of first chaetiger with a cirriform lobe (one paratype with a bifid tip); anterior chaetigers with long papillae, 2-3 postchaetal and two longitudinal rows of elongated cirriform ones.

Chaetiger 1 shorter than chaetigers 2-3, these with a conical, blunt notopodial lobe, larger than following ones. Chaetal transition from cephalic cage to body chaetae gradual; falcate, anchylosed hooks starting by chaetiger 21, by chaetiger 32 all neurochaetae anchylosed, falcate hooks (about chaetiger 40 in other anterior fragments). Gonopodial lobes not visible (externally detectable by a low rounded hump in chaetiger 5; tunic removed from one specimen UMML; gonopodial lobes present in chaetiger 5, each conical, blackish, with a thin projection reaching the tunic outer surface).

Parapodia well developed, placed on the body corners. Median neuropodia ventrolateral. Notopodia long, lobate, with 2-3 cirriform postchaetal papillae. Neuropodia long lobes, with two long postchaetal papillae. Noto- and neuropodia well separated from each other.

Median notochaetae arranged in short transverse series, 7-8 per bundle, as long as ½ body width; all notochaetae multiarticulated capillaries, short articles basal and medially, long articles restricted distally (Fig. 4G). Neurochaetae multiarticulated capillaries in anterior chaetigers, replaced by hooks from chaetiger 21, where one falcate simple hook appears; by chaetiger 32, all neurochaetae anchylosed, falcate hooks; median and posterior hooks subdistally expanded, spoon-shaped, tip acute, entire (Fig. 4H). Neurochaetae arranged in transverse series, 6-8 per neuropodium, five in posterior chaetigers, short anchylosed articles or rings present to the subdistal region.

Posterior region slightly tapered, chaetae smaller (Fig. 4E); pygidium with anus ventral, a dorsal wide rounded lobe, no anal cirri.

REMARKS

Buskiella McIntosh, 1885 has multiarticulate, long chaetae in both parapodial rami (Salazar-Vallejo & Zhadan 2007). *Buskiella borealis* Hartman, 1965 does not fit into this genus because it has a tongue-shaped branchial plate and anchylosed neurochaetae. Consequently, it is transferred here to *Trophoniella*.

As stated above, *T. borealis* n. comb. is closely allied to *T. bastidai* n. sp. They differ because in *T. borealis* n. comb. the notopodial lobes are restricted to chaetigers 2-3, whereas in *T. bastidai* n. sp. they reach chaetiger 5, being larger in chaetigers 3-5, and the cephalic cage has less chaetae (5-7 per bundle) than in *T. bastidai* n. sp. (14-18 per bundle).

Trophoniella capitata (Nonato, 1966) n. comb.
(Fig. 5)

Pherusa capitata Nonato, 1966: 71-73, figs 10-12.

Stylarioides rudis Grube & Müller *in* Grube, 1877: 67 (type locality: Brazil, Desterro), 71 *partim*. — Hartwich 1993: 134 *partim*.

MATERIAL EXAMINED. — Non-type specimen (ZMB unnumb.), off Florianopolis (*olim* Desterro), Santa Catharina Island, Brazil, F. Müller (no further data).

DISTRIBUTION. — Southern Brazil, in shallow water soft bottoms. Nonato (1966) provided measurements for a single specimen collected close to the type locality, off Barra de Rio Grande (32°05'S, 51°48'W), in 18 m, muddy bottom. He stated that he had other specimens from Ubatuba, Brazil, but beyond the chaetiger number, nothing is said about variation; perhaps he was dealing with different species. Type material was not available. The type material of *S. rudis* was collected in Desterro, which is now called Florianopolis (27°30'S, 48°30'W), Santa Catharina Island, Brazil, where most of Müller's specimens came from, but there are no more data.

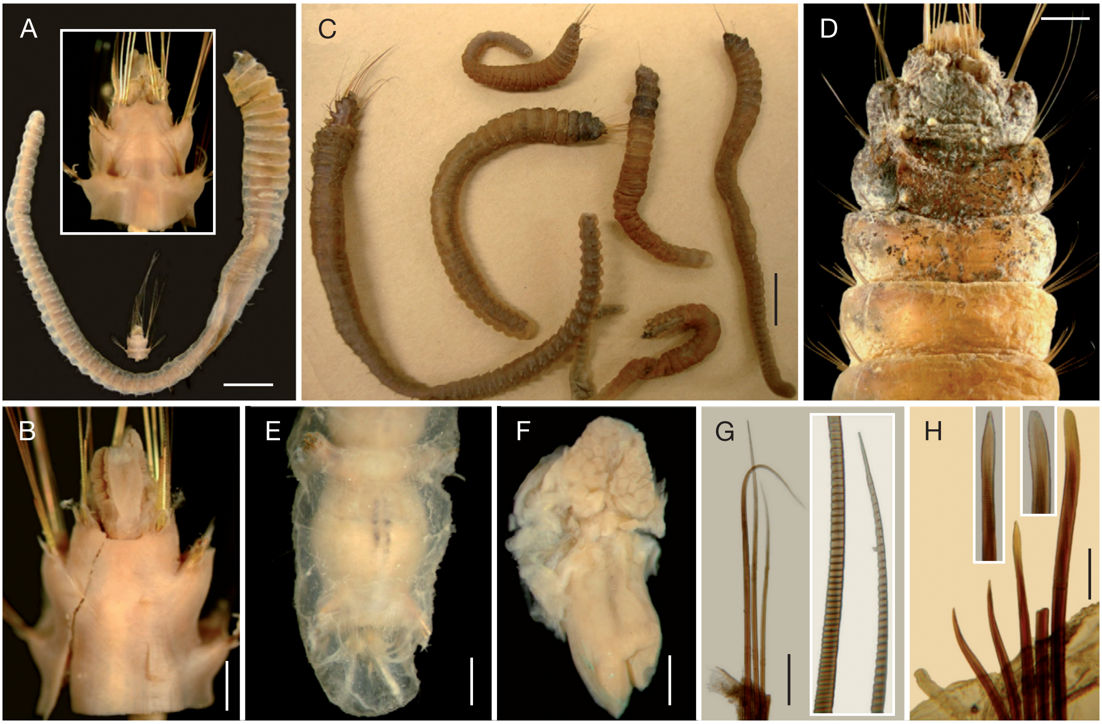

FIG. 4. — *Trophoniella borealis* (Hartman, 1965) n. comb.: **A**, holotype (LACM-AHF 544), first three chaetigers removed (insert: anterior end, dorsal view); **B**, same, anterior end, ventral view, oral tube and palps exposed; **C**, paratypes (LACM-AHF 545); **D**, paratype, anterior end, dorsal view; **E**, another paratype, posterior end, ventral view; **F**, another paratype, head, branchiae and palps detached; **G**, another paratype, chaetiger 10, notopodium (insert: enlarged basal and distal notochaetal regions); **H**, same, chaetiger 32, neurochaetae (inserts: expanded tips of larger neurohooks). Scale bars: A, 9 mm; B, 1 mm; C, 1.2 mm; D, 1.6 mm; E, 0.6 mm; F, 0.4 mm; G, 0.5 mm; H, 200 µm.

DESCRIPTION

Body complete (Fig. 5A), tapering posteriorly, slightly damaged, 25.5 mm long, 3 mm wide, cephalic cage 3 mm long, 68 chaetigers. Tunic papillated, with large sediment particles on dorsal (Fig. 5B) and ventral surfaces (Fig. 5C), not completely covering the body surface, sediment especially abundant dorsally and anteriorly; posteriorly almost bare. Papillae sparse, clavate, longer on chaetal lobes.

Cephalic hood slightly exposed, short, margin apparently smooth. Anterior end structure not studied; not dissected to avoid further damage. Some cirriform branchiae exposed, stemming from a tongue-like protuberance.

Cephalic cage chaetae as long as body width. Chaetigers 1-3 involved in the cephalic cage; chaetae arranged in short ventrolateral series; notopodia with 7-8 chaetae, neuropodia with 8, 7, 6 chaetae. Anterior dorsal margin of first chaetiger with a median trifid lobe, projected anteriorly (median tine lost). Anterior chaetigers without especially long papillae. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt; chaetal type change in chaetiger 5. Gonopodial lobes not seen.

Parapodia lateral, poorly developed, chaetae emerging from the body wall. Median neuropodia ventrolateral. Noto- and neuropodia short, chaetal lobes with few papillae; notopodia with three papillae: two shorter, prechaetal, placed towards the border of the chaetal series, another larger papilla, postchaetal, placed by the middle of the chaetal series. Neuropodia with three papillae of about the same size, one prechaetal, placed about the middle of the chaetal series, two postchaetal papillae placed towards the border of the chaetal series. Noto- and neuropodia close to each other.

Median notochaetae arranged in short transverse series, about seven notochaetae per bundle, as long as ⅓ body width; all notochaetae multiarticulated capillaries, articles short basally, medium-sized medially, longer distally (Fig. 5D). Neurochaetae multiarticulated capillaries in chaetigers 1-3, articles short. Bidentate neurohooks with long articles, in chaetigers 4-27 (Fig. 5E, insert), 4-5 per bundle, each with distal piece longer, bidentate, accessory tooth flat, sometimes longer than main tooth. Posterior chaetigers with anchylosed, bidentate hooks, distally smooth, less pigmented (Fig. 5E); 4-5 per bundle, each subdistally straight, bidentate, with main tooth falcate, thick, accessory tooth flat, sometimes longer than main one, rings short, present to the subdistal region.

Posterior end tapering to a blunt tip; pygidium with anus ventral, without anal cirri.

REMARKS

Trophoniella capitata n. comb. resembles *T. fauveli* n. sp. from Egypt: both have large, spread apart sediment particles on dorsal and often lateral surfaces, and their anchylosed neurohooks start in median chaetigers. There are two main differences between them: the presence of notopodial lobes and the start of anchylosed neurohooks. Thus, there are no notopodial lobes in *T. capitata* n. comb. and its anchylosed neurohooks start by chaetiger 28, whereas in *T. fauveli* n. sp., notopodial lobes are present and its anchylosed neurohooks start by chaetiger 40.

The type material of *Stylarioides rudis* from the ZMB contains specimens of two different species; three specimens belong to *T. rudis* n. comb. (redescribed below), and the other one is conspecific with *T. capitata* n. comb. In the original diagnosis of *S. rudis*, nothing was stated about the sediment grains cover, which indicates that Grube concentrated on those specimens without sediment. Because Grube (1877) used the sediment grains cover to group his species, especially if they were cemented over the anterior end, then it can be concluded that he did not study this specimen in enough detail. Further, it seems that when Nonato (1966) described *Pherusa capitata*, he overlooked Grube's paper; his species name is retained because the specimen from the type lot differs from those which were used to diagnose *S. rudis* and fits with *T. capitata* n. comb. This choice has been made with hesitation and the final decision requires topotype materials; regretfully, type materials for some of Nonato species are very difficult to find (P. C. Lana, pers. comm., Oct. 2004).

Trophoniella chilensis
(Hartman, 1967) n. comb.
(Fig. 6)

Therochaetella chilensis Hartman, 1967: 128, 129, pl. 37, fig. C (not D) *partim.* — Rozbaczylo 1985: 161.

TYPE MATERIAL. — **Chile**. Holotype of *Therochaetella chilensis* (USNM 55550) and 2 paratypes (USNM 55551), R/V *Eltanin*, stn 753 (33°16'S, 71°47'W), 192 m, 26.IX.1963, with a ventral oblique dissection (paratypes of *T. chilensis* 2 anterior fragments and 2 median pieces; one is probably an undescribed species of *Bradabyssa* Hartman, 1967 but too damaged [see remarks]; anterior fragment 6 mm long, 1.6 mm wide, cephalic cage 4 mm long, 19 chaetigers).

DISTRIBUTION. — Only known from the type locality, off Santiago, Chile, in 192 m.

REDESCRIPTION

Holotype (USNM 55550) complete (Fig. 6A). Tunic papillated, with many large sand particles dorsally (Fig. 6B) and ventrally, particles immersed in the tunic, without sediment particles along the posterior region. Body cylindrical, posteriorly tapered, 29 mm long, 2.5 mm wide, cephalic cage 6 mm long, 88 chaetigers (regenerating from chaetiger 71). Body papillae arranged in longitudinal rows; chaetigers 1-3 with slightly enlarged dorsal tubercles, posteriorly not significantly larger than other papillar lobes.

Anterior end not exposed in holotype; dissection not modified to avoid any further damage (Fig. 6C). Paratype with anterior end not exposed, but dissected. Prostomium low with two large circular, black eyes. Palps small. Branchiae cirriform, thick, about 42 pairs, placed over a short tongue-like plate. Nephridial lobes not seen.

Cephalic cage chaetae twice as long as body width. First three chaetigers involved in the cephalic cage;

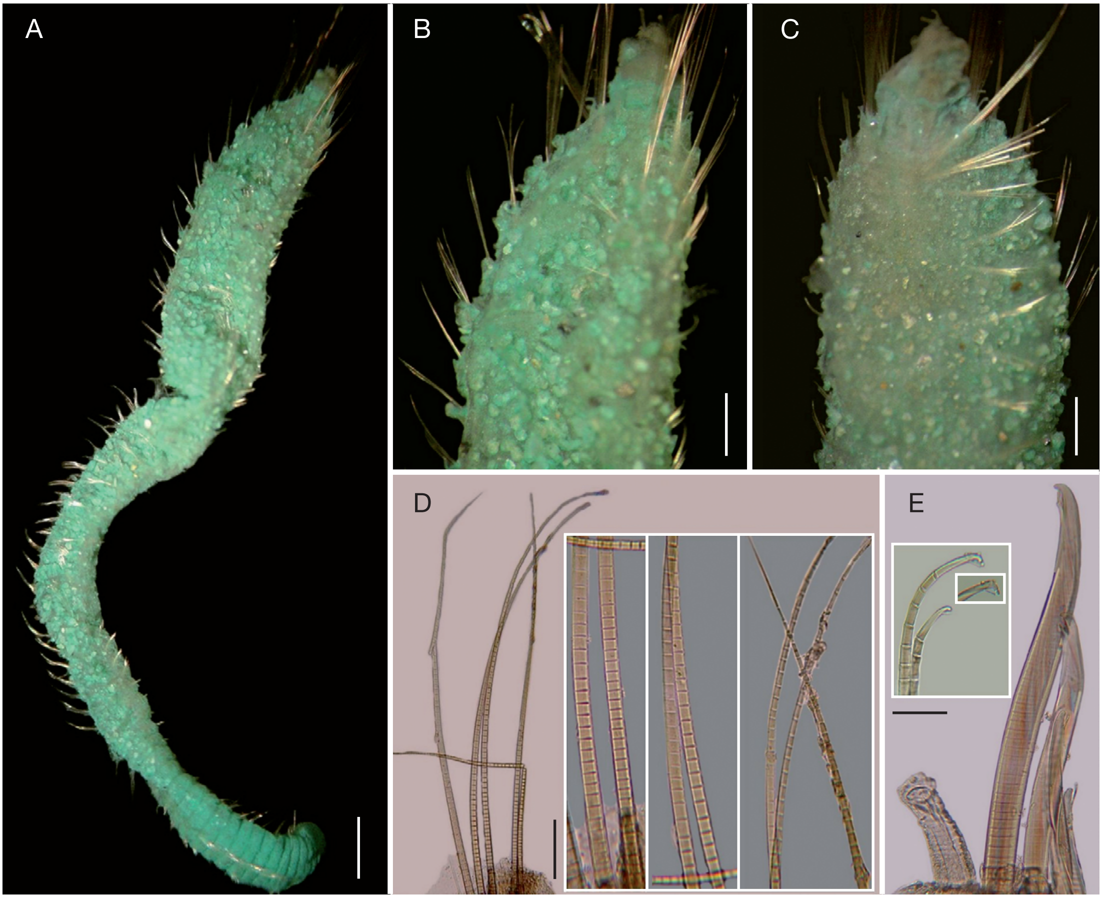

FIG. 5. — *Trophoniella capitata* (Nonato, 1966) n. comb., non-type specimen (ZMB unnumb.): **A**, dorsal view; **B**, anterior end, dorsal view; **C**, anterior end, ventral view; **D**, chaetiger 11, notopodium (insert: basal, medial and distal notochaetal regions); **E**, chaetiger 32, neurochaetae (insert: chaetiger 11, neurochaetal tips). Scale bars: A, 2 mm; B, 0.9 mm; C, 0.75 mm; D, 112 μm; E, 50 μm.

chaetae progressively smaller; 4-5 chaetae per bundle. Anterior dorsal margin of first chaetiger with a trilobed, small projection; anterior chaetigers with long, dorsolateral papillae (better preserved in paratype); posterior chaetigers with three rows of elongated papillae, each segment with three papillae, one middorsal and two dorsolateral. Chaetal transition from cephalic cage abrupt. Chaetal type changing in chaetiger 5, neurochaetae slightly thicker than notochaetae. Second neurochaetal type changing by chaetiger 25 (most chaetae broken, so it is difficult to be precise), anchylosed neurohooks thick. No gonopodial lobes; two ventral rows of single elongated papillae.

Parapodia better developed on first few chaetigers, posteriorly reduced. Noto- and neuropodia lateral. Notopodia with few long, postchaetal papillae, especially on anterior chaetigers. Up to three papillae per bundle, the median one the largest. Each papilla long, capitate.

Median notochaetae in short transverse series, six per bundle, as long as ½-⅔ body width; all notochaetae multiarticulated, basal articles short, long medially and distally (Fig. 6D). Median neuropodia ventrolateral; each with a postchaetal capitate papilla. Neurochaetae mostly bidentate, accessory tooth often eroded. Multiarticulate neurochaetae in chaetigers 1-*c.* 25; anchylosed neurohooks from

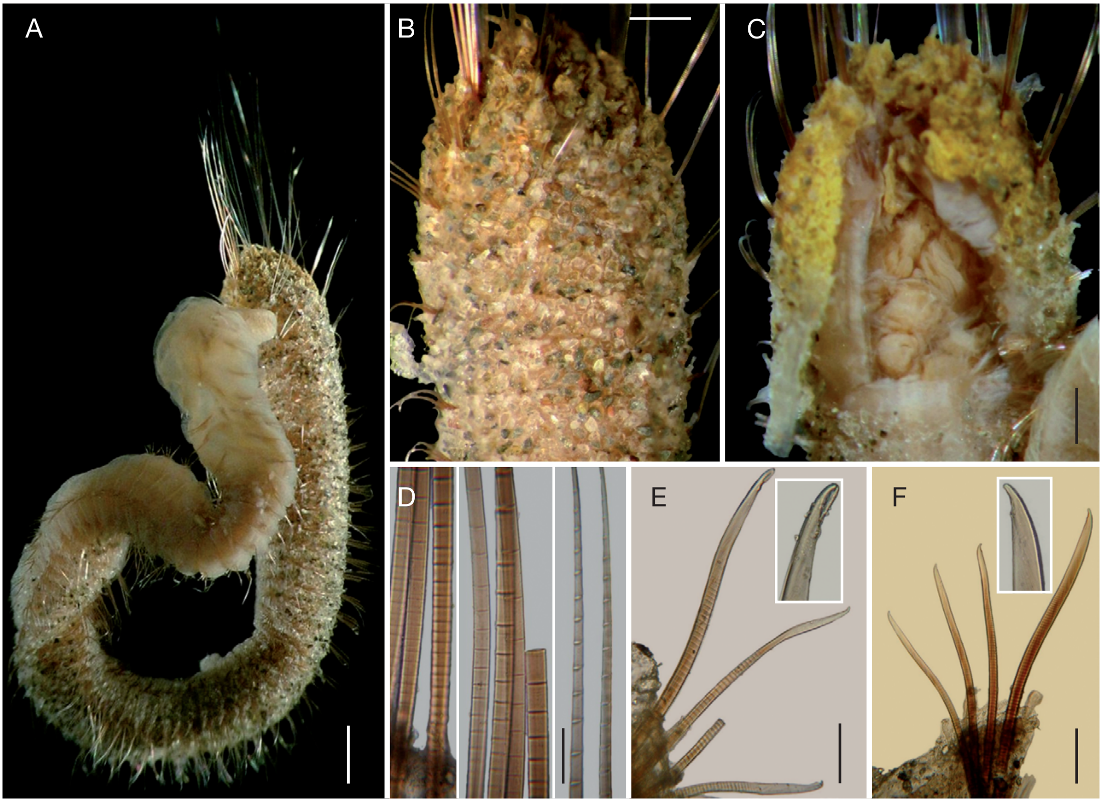

Fig. 6. — *Trophoniella chilensis* (Hartman, 1967) n. comb.: **A**, holotype (USNM 55550), dorsal view; **B**, same, anterior end, dorsal view; **C**, same, anterior end, ventral view; **D**, paratype (USNM 55551), chaetiger 17, basal, medial and distal notochaetal regions; **E**, same, chaetiger 19, neurochaetae (insert: largest chaetal tip); **F**, holotype, chaetiger 33, neurochaetae (insert: largest chaetal tip). Scale bars: A, 1.2 mm; B, 0.5 mm; C, 0.4 mm; D, 112 µm; E, 70 µm; F, 150 µm.

around chaetiger 25; five multiarticulated capillaries in anterior neuropodia, 4-5 hooks in median and posterior neuropodia, arranged in transverse or slightly oblique series, each subdistally straight, with short articles continued to the subdistal region; tips bidentate (Fig. 6E), accessory tooth often eroded to small humps (Fig. 6F).

Posterior end in regeneration; pygidium without anal cirri; anus dorsoterminal.

Remarks

Trophoniella chilensis n. comb. belongs to the group provided with anchylosed neurohooks in median chaetigers and a tunic with large sediment particles. It is unique because the particles are completely immersed in the tunic giving a smooth profile, whereas in the other species they are not completely covered by the tunic, giving a rough profile.

Trophoniella ehlersi (Day, 1973) n. comb.
(Fig. 7)

Pherusa sp. – McCloskey 1970: 26.

Pherusa ehlersi Day, 1973: 107, 108, fig. 14g-j.

Type material. — **Northwestern Atlantic Ocean, eastern United States.** Holotype (USNM 43133), off Beaufort, North Carolina, Lookout outcrop, in corals, 18.3 m, 7.IX.1966, R. McCloskey (1 smaller specimen in the same vial belongs to the same species; 3.5 mm long, 0.7 mm wide, cephalic cage 2 mm long, 25 chaetigers).

ADDITIONAL MATERIAL. — **Northwestern Atlantic Ocean, eastern United States.** 1 complete specimen (USNM 107986), off North Carolina, R/V *Onslow Bay*, stn IS05 (32°24'06"N, 76°35'W), 18 m, 11.III.1981, identified by L. Wood (14 mm long, 3.5 mm wide, cephalic cage 3 mm long, 60 chaetigers; mature ♀, previously dissected ventrally, and with another longitudinal cut anterodorsally; anterior end missing; the latter was used to remove a portion of the dorsal outer cover and examine the surface of the anterior chaetigers). — 1 specimen (USNM 107987), complete, off South Carolina, R/V *Bagby*, stn IS01 (32°29'36"N, 79°42'30"W), 19 m, 21.I.1980, Roland & Knott id. (14 mm long, 4 mm wide, cephalic cage 3 mm long, 52 chaetigers; mature ♀, previously dissected throughout the anterior end; anterior end missing; parapodia removed to see chaetae).

Gulf of Mexico. 1 specimen (MCZ 1205), dried out, 400 m S off Sand Key, Florida, 18 m, 27.I.1868, L. F. de Pourtalès. — 1 specimen (ECOSUR), Isla de Enmedio, Veracruz, Mexico, in sponge (*Ircinia strobilina*), 5 m, III.1992, L. Carrera (15 mm long, 2 mm wide, cephalic cage 4 mm long, 56 chaetigers). — 1 specimen (ECOSUR), off Ria Lagartos, Yucatan, Mexico, 3 m, calcareous rock, 18.II.1999, R. Bastida & S. I. Salazar-Vallejo (16 mm long, 2.5 mm wide, cephalic cage 3 mm long, 49 chaetigers). — 1 specimen (ECOSUR), juvenile, distorted, apparently regenerating the posterior end, off San Felipe, Yucatan, Mexico, 2 m, calcareous rock, 19.II.1999, S. I. Salazar-Vallejo (6 mm long, 1 mm wide, cephalic cage 3 mm long, 32 chaetigers).

Caribbean Sea. 1 specimen (ECOSUR), Punta Nizuc, Quintana Roo, calcareous rock, 3 m, 31.VIII.1997, L. Carrera (7 mm long, 1.5 mm wide, cephalic cage 3 mm long, 36 chaetigers). — 1 specimen (ECOSUR), Punta Herradura, Quintana Roo, coral rock, 2 m, 28.X.1997, L. Carrera & S. I. Salazar-Vallejo (10 mm long, 2 mm wide, cephalic cage 3 mm long, 44 chaetigers; papillae tips pale). — 2 specimens (ECOSUR), 1 complete and an anterior fragment, Buenavista, Xahuayxol, Quintana Roo, Mexico, coral rock, 1 m, 31.X.1997, L. Carrera & S. I. Salazar-Vallejo (complete 12 mm long, 3 mm wide, cephalic cage broken, 4 mm long, 57 chaetigers). — 1 specimen (ECOSUR), Camping, Isla Contoy, Quintana Roo, Mexico, coral rock, 1 m, 22.II.1999, S. I. Salazar-Vallejo (18 mm long, 1.5 mm wide, cephalic cage 2 mm long, 49 chaetigers). — 1 specimen (ECOSUR), Majagual, Quintana Roo, Mexico, coral rock, 1 m, XII.2000, P. Salazar (19 mm long, 2 mm wide, cephalic cage 4 mm long, 50 chaetigers). — 1 specimen (ECOSUR), Punta Nizuc, Quintana Roo, Mexico, coral rock, 4 m, 10.II.2001, S. I. Salazar-Vallejo (14 mm long, 3 mm wide, cephalic cage 4 mm long, 52 chaetigers). — 2 specimens (ECOSUR), 1 complete and an anterior fragment with head exposed, Rio Indio, Quintana Roo, coral rock, 17.III.2001, L. Carrera (complete 14 mm long, 2 mm wide, cephalic cage 3 mm long, 44 chaetigers). — 5 specimens (ECOSUR), larger regenerating median and posterior regions, Xcacelito, Quintana Roo, Mexico, mixed bottom (rock and sand), 1 m, 26.X.2002, L. Carrera, P. Salazar & M. Londoño (11-24 mm long, 2.0-3.0 mm wide, cephalic cage 3-4 mm long, 44-57 chaetigers; papillae tips pale). — 3 specimens (LACM-AHF 2482), Panama, Bocas del Toro Archipelago, Laguna de Chiriqui, Isla Aqua (9.178°N, 82.054°W), northwest side, from chunks of Teredo-bored wood, among coral rubble and silty sand, 20-25 ft, SCUBA, 8.VIII.2003, W. Keel & L. Harris (5-13 mm long, 1 mm wide, cephalic cage 1.3 mm long, 38-44 chaetigers).

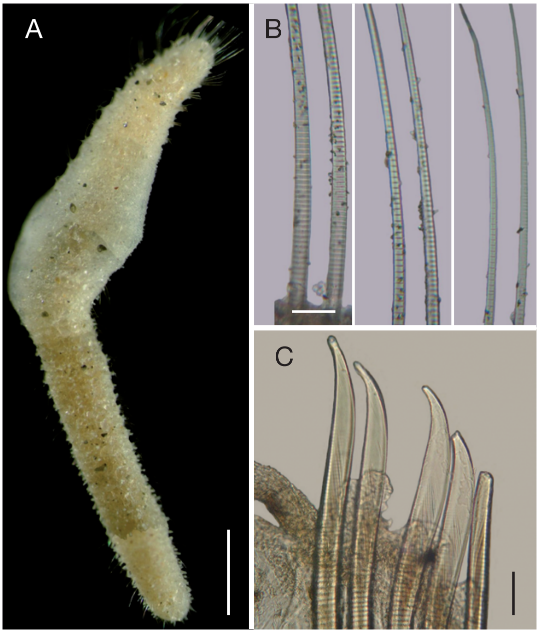

FIG. 7. — *Trophoniella ehlersi* (Day, 1973) n. comb.: **A**, holotype (USNM 43133), dorsal view; **B**, same, chaetiger 10, notochaetal basal, median and distal regions; **C**, non-type specimen (USNM 107987), chaetiger 44, neurochaetae. Scale bars: A, 2.25 mm; B, 60 µm; C, 45 µm.

DISTRIBUTION. — From the southeastern United States to the southwestern Caribbean Sea, in shallow water (1-20 m), mixed bottoms.

DESCRIPTION

Holotype (USNM 43133) cylindrical, blunt, slightly compressed anteriorly, tapering posteriorly (Fig. 7A), 13 mm long, 1.8 mm wide, cephalic cage 3 mm long, 50 chaetigers (some parapodia previously removed). Tunic papillated, with fine sediment particles dorsally and ventrally.

Anterior end not exposed; not dissected to avoid further damage. Cephalic cage chaetae ⅓ longer than body width. Chaetigers 1-3 involved in the cephalic cage. Chaetiger 4 with notochaetae long, more or less directed anteriorly but half as long as those in chaetiger 3. Cephalic cage chaetae arranged in a short series; each chaetiger with 3-4 chaetae, slightly more abundant ventrally.

Anterior dorsal margin of first chaetiger with a median, digitate papillae; anterior chaetigers with long, digitate, dorsolateral papillae in additional to notopodial ones. Chaetal transition from cephalic cage to body chaetae abrupt; chaetal change in chaetiger 4 with shorter notochaetae; anchylosed neurohooks from chaetiger 5. Gonopodial lobes not seen.

Parapodia poorly developed; chaetae emerging from the body wall. Noto- and neuropodia on body corners. Notopodia with two large digitate papillae per bundle, one on chaetal base, the other postchaetal.

Median notochaetae arranged in short transverse series, 3-4 per bundle, each as long as half body width; all notochaetae multiarticulated capillaries, articles short basally and medially, distally medium-sized (Fig. 7B). Median neuropodia ventrolateral. Neuropodia with digitate papillae, shorter than notopodial ones; one postchaetal papilla. Neurochaetae multiarticulated capillaries in chaetiger 4; from chaetiger 5, 4(-5) falcate hooks, tips entire; arranged in slightly oblique series, short rings present to the median region (Fig. 7C).

Posterior end a low cone; pygidium without anal cirri, but two dorsal, long papillae.

REMARKS

Trophoniella ehlersi n. comb. resembles *T. grandis* n. comb. because both species have fine sediment particles over the dorsal and ventral surfaces. They differ because in *T. ehlersi* n. comb. the anterior chaetigers do not have dorsal tubercles or notopodial lobes, whereas in *T. grandis* n. comb. there are dorsal tubercles in the first few chaetigers, and because in *T. ehlersi* n. comb. the falcate neurohooks start by chaetiger 5 whereas they start by chaetiger 7 in *T. grandis* n. comb.

McCloskey (1970) specimens were used for the original description; they were associated to a small tree-like scleractinian (*Oculina arbuscula* Agassiz, 1864). The branching pattern of this coral allows some sedimentation on it; the polychaetes may have been found there, or in the sediment at the base of the coral. The finding of only four specimens by McCloskey, despite a very intensive sampling, precluded any ecological analysis on the species.

Trophoniella eliasi n. sp.
(Fig. 8)

Pironis [*sic*] *arenosus* – Rullier & Amoureux 1979: 183 (*non* Kinberg 1867).

TYPE MATERIAL. — **Southwestern Atlantic Ocean**. Holotype (MACN 39283), R/V *Chairpesca 57* cruise, off Puerto Madryn, Argentina, in stomach contents of a ♂ "gatuzo" or fine-tailed shark, *Mustelus schmitti* Springer, 1939, 65 cm long, caught in 117 m water depth, 26.IX.2005.

ADDITIONAL MATERIAL. — **Southwestern Atlantic Ocean**. 6 specimens (MACN), 1 anterior and 5 median fragments, apparently not matching, stomach contents of a ♀ "gatuzo" or fine-tailed shark, *M. schmitti*, 56 cm long, off Siempre San Salvador, Puerto Madryn, Argentina, 22.VI.2005 (anterior fragment with sediment cover, most chaetae broken); 1 specimen (MACN), anterior fragment, stomach contents of a ♀ "gatuzo" or fine-tailed shark, *M. schmitti*, 76 cm long, off Siempre San Salvador, Puerto Madryn, Argentina, 31.VIII.2005 (37 mm long, 5 mm wide, cephalic cage broken, 41 chaetigers; dissected for anterior end); 1 specimen (MACN), without anterior end, broken in 3 fragments, stomach contents of a ♂ "gatuzo" or fine-tailed shark, *M. schmitti*, 74 cm long, San Salvador, Puerto Madryn, Argentina, 31.VIII.2005 (30 + 10 + 75 mm long, 27 + 9 + 94 chaetigers). — 1 specimen (MACN), anterior fragment, off Puerto Madryn, Viernes Santo, *Rede 04* cruise, stn 6 (41°08'S, 64°09'W), stomach contents of a ♀ "gatuzo" or fine-tailed shark, *M. schmitti*, 82 cm long, caught in 99 m water depth, 30.X-1.XI.2006. — 1 specimen (MACN), broken in 2, damaged, off Puerto Madryn, Siempre San Salvador, stomach contents of a ♀ "pescadilla" or sea trout, *Sympterigia bonapartei* Müller & Henle, 1841, 52 cm long, 110 m depth, 18.V.2007 (73 mm long, 5 mm wide, cephalic cage missing, about 55 chaetigers); 1 specimen (MACN), anterior fragment, damaged, off Puerto Madryn, Siempre San Salvador, stomach contents of a ♀ "gatuzo" or fine-tailed shark, *M. schmitti*, 88 cm long, 16.VIII.2007. — 3 specimens (MACN), an anterior and 2 median fragments, damaged, off Puerto Madryn, Siempre San Salvador, stomach contents of a ♀ "gatuzo" or fine-tailed shark, *M. schmitti*, 70 cm long, 110 m depth, 16.VIII.2007. — 1 specimen (MNHN

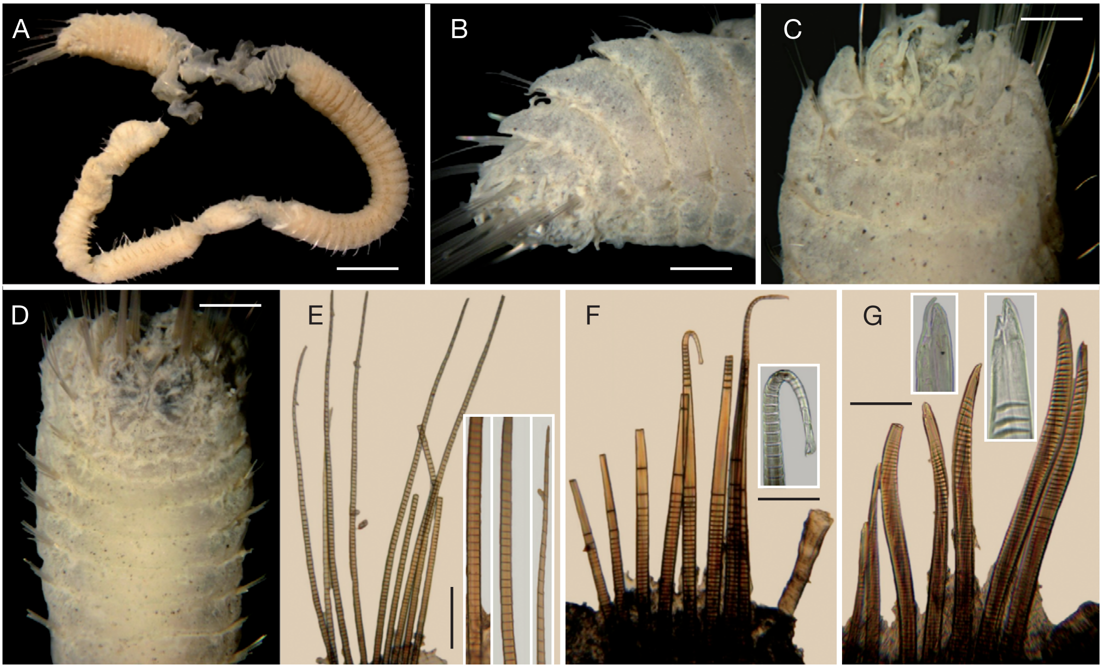

FIG. 8. — *Trophoniella eliasi* n. sp., holotype (MACN 39283): **A**, lateral view; **B**, anterior end, lateral view; **C**, anterior end, dorsal view; **D**, anterior end, ventral view; **E**, chaetiger 30, notopodium (insert: notochaetal basal, medial and distal regions); **F**, chaetiger 30, neuropodium (insert: central neurochaeta tip); **G**, chaetiger 52, neuropodium (inserts: tip of neurochaetae showing complete and eroded accessory tooth). Scale bars: A, 4 mm; B, 0.7 mm; C, 0.6 mm; D, 0.85 mm; E, 160 µm; F, 140 µm; G, 100 µm.

884), anterior fragment, flaccid, probably preserved in ethanol, with a dissection along the anterior end, off Nova Iguasu, R/V *Calypso*, stn 108 (23°07'S, 43°11'W), 54 m, 7.XII.1961. — 1 specimen (MNHN 884), flaccid, probably preserved in ethanol, without posterior end, off Rio Grande, R/V *Calypso*, stn 154 (32°15'S, 51°58'W), 18 m, 20.XII.1961.

TYPE LOCALITY. — Off Puerto Madryn, in soft bottoms, in about 120 m depth.

DISTRIBUTION. — Apparently restricted to the central portion of Argentina, off Puerto Madryn, in soft sediments in 99-117 m depth, a frequent prey of some demersal fishes.

ETYMOLOGY. — The specific name is to honor Dr Rodolfo Elías, an Argentinian colleague who has concentrated his efforts on benthic ecology, and has made several publications on polychaete systematics from northern Argentina.

DESCRIPTION

Holotype (MACN 39283) without posterior end, breaking in parts, stiff, swollen anteriorly, softer, tapering posteriorly (Fig. 8A), 91 mm long, 4 mm wide, cephalic cage (broken) 7 mm long, 86 chaetigers. Tunic completely covered with fine sediment particles (Fig. 8B, C), particles sparsely distributed, most particles removed by digestion (a non-type specimen with densely packed sediment grains, most chaetae broken). Body papillae mostly eroded; parapodial papillae long, capitate; dorsal papillae not forming tubercles; ventral papillae forming two longitudinal rows.

Anterior end not exposed, observed by dissection of a non-type specimen. Macerated. Cephalic hood short, smooth, margin papillose. Prostomium low, blackish. Eyes not seen. Caruncle well developed, probably extended along the whole branchial plate, median keel thick, wide, pale, lateral ridges darker. Palps lost, size-relationship with branchiae unknown, palp keels pale, rounded. Lips well developed, distorted by pharynx eversion. Branchiae maculated, cirriform, sessile on a partially digested tongue-like protuberance (posterior margin unknown), arranged in two lateral groups, in 5-6 longitudinal rows per group, with about 60 filaments per group; few filaments remaining. Nephridial lobes not seen.

Cephalic cage chaetae about twice as long as body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short series, dorsolateral in chaetiger 1, lateral in chaetiger 2; chaetiger 1 with 12 noto- and 10 neurochaetae per side; chaetiger 2 with about eight chaetae per bundle.

Anterior dorsal margin of first chaetiger with a macerated, median, single, thin lobe (Fig. 8C), projected anteriorly (trifid in a non-type specimen), marginal papillae not seen. Anterior chaetigers (2-4) with large notopodial lobes and long, inferior notopodial papillae, directed anteriorly, diminishing in size posteriorly. Chaetigers 1-3 becoming progressively longer. Chaetal transition from cephalic cage to body chaetae gradual; bidentate, multiarticulate neurohooks from chaetiger 5; neurohooks with anchylosed articles present from chaetiger 35. Gonopodial lobes not seen (Fig. 8D).

Parapodia better developed in anterior chaetigers; median and posterior ones with short notopodial lobes, chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Notopodia with two prechaetal papillae, one postchaetal smaller papilla; neuropodia with one prechaetal and three postchaetal papillae; inferior notopodial papillae better developed in anterior chaetigers.

Median notochaetae arranged in short oblique series, 9-10 per notopodium, as long as ¼ body width; all notochaetae multiarticulated capillaries, short articles basally, medium-sized medially, longer articles distally (Fig. 8E, insert). Neurochaetae multiarticulated capillaries in chaetigers 1-18, replaced by hooks from about chaetiger 20, each with a very long median article and shorter articles basally and distally, tips bidentate (Fig. 8F); by chaetiger 35, all neurochaetae anchylosed hooks (Fig. 8G). Neurochaetae arranged in transverse series, median region with 7-8 per neuropodium, six in posterior chaetigers. Anchylosed neurohooks bidentate (Fig. 8G, inserts), most with tips eroded, dark brown, distally tapering, less pigmented, with short rings continued to the subdistal region, most with tips broken, eroded, others with bidentate tips, accessory tooth acute, longer than fang.

Posterior end unknown.

Variation

The specimens were retrieved from the stomach contents of two different fish species, the "gatuzo" or fine-tailed shark, *M. schmitti*, the most frequent one, whereas the other, the "pescadilla" or sea trout, *S. bonapartei*, had a single specimen. The damage to the body was similar because most long chaetae were broken, whereas the sediment cover showed different degrees of particle removal, probably depending on how much time the polychaete had spent within the fish stomach. Thus, the body had different densities of particles although even those with fewer ones, retained the overall pattern throughout the body surface.

REMARKS

Trophoniella eliasi n. sp. resembles other species having fine sediment particles completely covering the body such as *T. harrisae* n. sp., *T. hospita* n. comb. and *T. orensanzi* n. sp. However, *T. eliasi* n. sp. differs from these three other species because it lacks dorsal tubercles, whereas the other species have them. It might be regarded that *T. eliasi* n. sp. is a smothered *T. orensanzi* n. sp. because the main difference is the lack of dorsal tubercles in the former. However, the tunic and its sediment cover in the corresponding region do not show any abrasion or fracture, and thus the lack of dorsal tubercles is a consistent difference between these two species. Further, these species are apparently living in different water depths; *T. eliasi* n. sp. was found in stomach contents of fishes caught in about 100 m depth, whereas *T. orensanzi* n. sp. thrives in shallow water, being found in about 9 m depth.

Trophoniella enigmatica n. sp.
(Fig. 9)

Stylarioides eruca – Fauvel 1934: 49 (*non* Claparède 1869).

TYPE MATERIAL. — **Mediterranean Sea**, **Adriatic Sea**. Holotype ♀ (MNHN A457), off Rovigno, Croatia, stn 83 (no further data), A. Vatova.

ADDITIONAL MATERIAL. — **Eastern Atlantic**. 1 specimen (MNHN 457), complete, Concarneau, France, 23.V.1923, P. Fauvel (39 mm long, 2.5 mm wide, cephalic cage 5 mm long, 68 chaetigers; 6-7 notochaetae per bundle in median

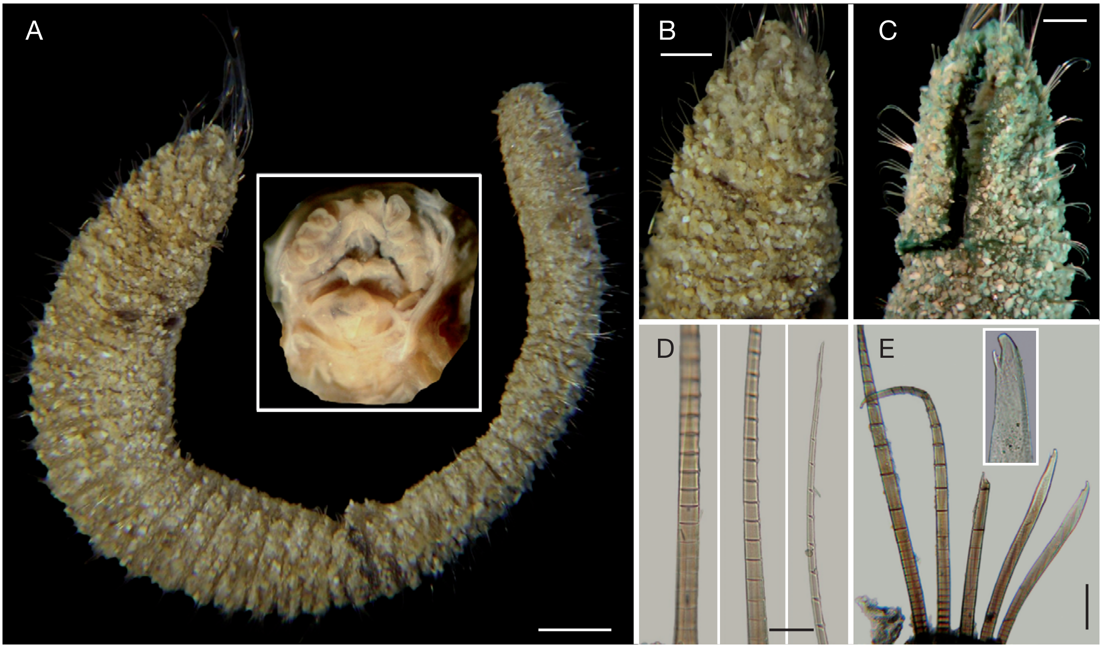

FIG. 9. — *Trophoniella enigmatica* n. sp., holotype (MNHN A457): **A**, dorsal view (insert: dissected head, branchiae and palps removed); **B**, anterior end, dorsal view; **C**, anterior end, ventral view; **D**, chaetiger 13, basal, medial and distal notochaetal regions; **E**, chaetiger 48, neurohooks (insert: tip of anchylosed neurohook). Scale bars: A, 2 mm; B, C, 1 mm; D, 50 µm; E, 110 µm.

chaetigers; first anchylosed neurohooks in chaetiger 25; all neurohooks anchylosed from chaetiger 55). — 2 specimens (MNHN 508), anterior fragments, R/V *Andrée* 1922 expedition, stn 8, off Bretagne, France, M. Monod. **Adriatic Sea.** 1 specimen (ECOSUR), stn SJ7 (45°17'N, 13°16'E), 31 m, silty sand, 27.II.2003, B. Mikac, without posterior end, blackish anterior region extending for chaetigers 1 and 2; 1 specimen (ECOSUR), same data, but 18.XII.2003, anterior fragment, head with 10 branchial filaments, palps lost; 1 specimen (ECOSUR), same data, but 28.V.2003, mature ♀, without posterior end, broken in 3 pieces, oocytes 150-175 µm in diameter; 1 specimen (ECOSUR), same data, but 29.I.2004, anterior fragment, anterior end blackish extending for 5 or 6 chaetigers.

TYPE LOCALITY. — Off Rovinj, Croatia (Herzegovina), in shallow water.

DISTRIBUTION. — Apparently disjunt, living in the Atlantic western coast of France and in the upper Adriatic Sea, in shallow water.

ETYMOLOGY. — The specific name derives from the Latin word "enigma", meaning enigma, puzzle, or mystery. It is used as an adjective to indicate the unexpected branchial features, which differ from all other species in the genus.

DESCRIPTION

Holotype (MNHN A457) a mature female, posteriorly incomplete, breaking in two parts, many chaetae broken (Fig. 9A). Body subcylindrical, tapering posteriorly, 36 mm long, 4 mm wide, cephalic cage 5 mm long, 49 chaetigers. Tunic dorsally and ventrally covered by large sediment grains, not immersed in the tunic (only sand grains, no forams or molluscs shell fragments). Papillae long, capitate, sparse, arranged in longitudinal rows, three dorsally, four ventrally, difficult to detect because of the size and colour of the adherent particles.

Anterior end observed by dissection. Cephalic hood short, margin finely papillated. Prostomium low cone, eyes large, dark; caruncle poorly developed, not reaching the branchial plate posterior margin (Fig. 9A, insert). Palps large, corrugated; palp keels low, rounded. Branchiae cirriform, thick, arranged as a continuous row with 10 filaments, some branchiae as long as palps. Nephridial lobes placed between the branchial row and the prostomium, short, rounded.

Cephalic cage chaetae about ¾ as long as body width, arranged in short transverse series. Chaetigers 1-2 involved in the cephalic cage; 5-6 noto- and 6-7 neurochaetae per side. Anterior margin of chaetiger 1 with a cirriform lobe, partially eroded (Fig. 9B); anterior chaetigers with small dorsal tubercles and one elongated postchaetal papillae, larger in notopodia. Dorsal tubercles low, in chaetigers 2-9.

Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae gradual; multiarticulate neurohooks from chaetiger 2, decreasing in size to chaetiger 5. Falcate anchylosed hooks from chaetiger 40. Gonopodial lobes not seen (Fig. 9C).

Parapodia well developed, placed on the body corners. Median neuropodia ventrolateral. Notopodia elongate, lobate, with a single large, capitate postchaetal papilla.

Median notochaetae arranged in short transverse series, 7-8 per bundle, as long as ½ body width; all notochaetae multiarticulated capillaries, short articles basally, medium-sized medially, long distally (Fig. 9D). Neurochaetae multiarticulated capillaries in chaetiger 1, from chaetiger 2 multiarticulated bidentate neurohooks, shorter neurohooks appear by chaetiger 5. From chaetiger 40, falcate bidentate anchylosed neurohooks. By chaetiger 48, two out of five neurohooks anchylosed (Fig. 9E). Multiarticulate neurohooks arranged in short transverse series, 5-6 in anterior chaetigers, 4-5 in posterior ones; each with short anchylosed articles basally, long medially, medium-sized distally. Distal piece with fang curved, bidentate, accessory tooth reaching fang's tip, leaving a wide inner area (Fig. 9E, insert). Anchylosed neurohooks with short rings, continued to the subdistal slightly expanded region, blade unpigmented, bidentate, fang curved, accessory tooth straight, often eroded.

Posterior end unknown. Oocytes dark, about 150-175 µm in diameter.

Remarks

Trophoniella enigmatica n. sp. has been included in this genus because most of its morphological features fit the generic diagnosis. There is one discrepancy, however, and it relates to the branchial plate; in most species of the genus, the branchial plate is tongue-shaped with thin, abundant filaments separated in two lateral groups by a posteriorly prolonged caruncle. In *T. enigmatica* n. sp. the branchial plate is barely projected and there are instead 10 thick filaments, arranged in a single row, and the caruncle is reduced, not reaching the branchial plate's posterior margin. Nevertheless, the relative tunic development and especially the chaetal pattern, because this species has anchylosed neurochaetae in posterior chaetigers, indicates it must be placed in *Trophoniella*.

Besides the above differences, *T. enigmatica* n. sp. is more closely related to *T. indica* n. comb., n. stat., from the Indian Ocean. The main differences between them, besides the branchial features, are the relative start of anchylosed neurohooks, and the size relationships between the fang and accessory tooth; thus, in *T. enigmatica* n. sp. these neurohooks start by chaetiger 40, whereas they start by chaetiger 14 in *T. indica* n. comb., n. stat. and the accessory tooth is as long as fang in *T. enigmatica* n. sp., whereas it is longer than fang in *T. indica* n. comb., n. stat.

Several specimens were also recorded from the same region as the holotype, in stations 9, 17, 38, 41, 43, 83, 95, 98, 109, 123. Some of them might be kept in the Museo di Zoologia, Centro di Ateneo per i Musei, Università degli Studi di Padova, Italia (http://www.unipd.it/musei/zoologia/collezioni/rovigno.html). Regretfully, they were not available, such that there is no way to precise which belong to the same species.

Trophoniella fauveli n. sp.
(Fig. 10)

Stylarioides eruca – Fauvel 1937: 34 (*non* Claparède 1869).

Type material. — **Mediterranean Sea**. Holotype (MNHN 406), off Alexandria, Egypt, stn 61, 50 fathoms, mud, 30.X.1933, A. Steuer.

Type locality. — Off Alexandria, Egypt, in muddy bottoms at 100 m depth.

Distribution. — Only known from the type locality in the eastern Mediterranean Sea, in muddy sediments at 100 m depth.

Etymology. — This species is named to honor the late Dr Pierre Fauvel, who devoted his life to the study of

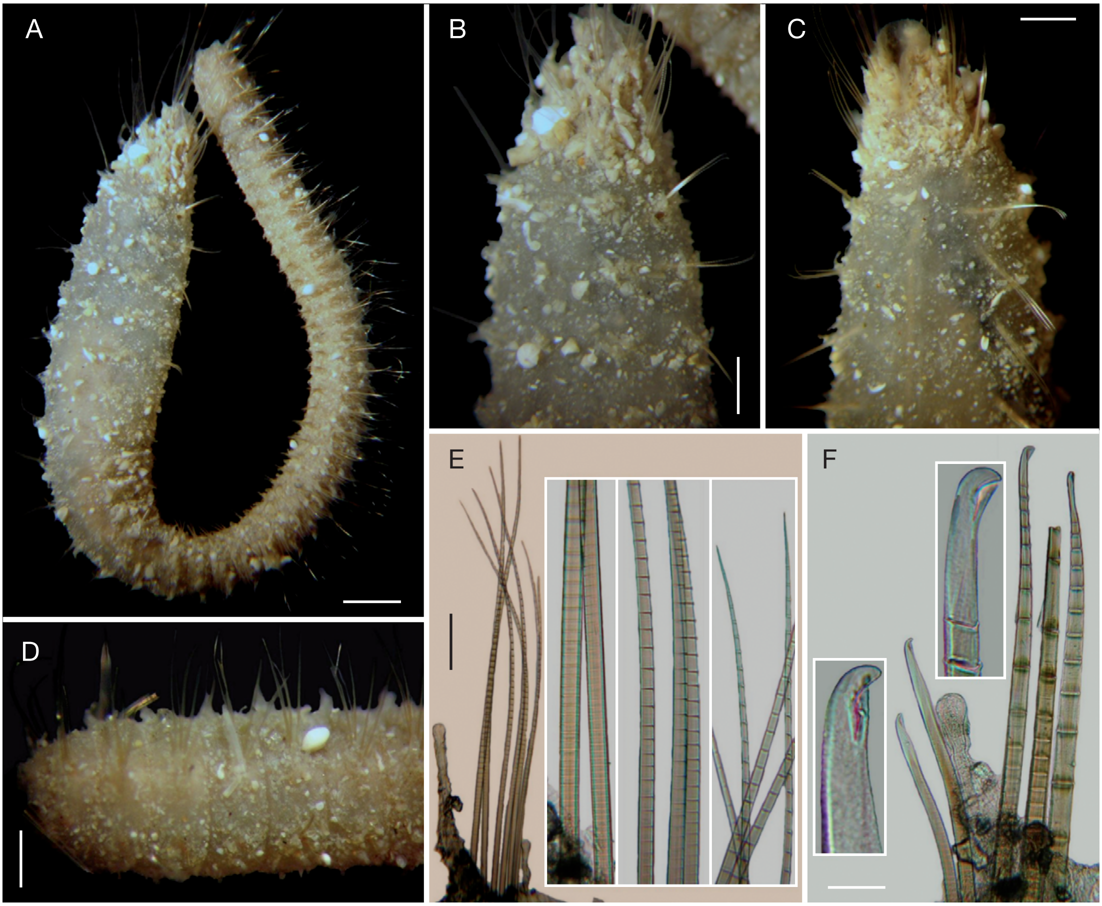

FIG. 10. — *Trophoniella fauveli* n. sp., holotype (MNHN 406): **A**, dorsal view; **B**, anterior end, dorsal view; **C**, anterior end, ventral view; **D**, posterior region, lateral view; **E**, chaetiger 16, notopodium (insert: basal, medial and distal notochaetal regions); **F**, chaetiger 33, neurochaetae (inserts: tips of chaetae). Scale bars: A, 1.5 mm; B, C, 0.85 mm; D, 0.6 mm; E, 225 µm; F, 80 µm.

polychaetes from all over the world, and especially for his relevant contributions to the Mediterranean fauna.

DESCRIPTION

Holotype (MNHN 406), cylindrical, tapering posteriorly (Fig. 10A), without posterior end, soft, apparently fixed in alcohol, 29 mm long, 3 mm wide, cephalic cage 8 mm long, 49 chaetigers. Tunic papillated, with sparse sediment grains dorsally and ventrally (Fig. 10B-D), slightly more densely covered in median and posterior chaetigers. Larger papillae forming longitudinal series, two dorsal and two ventral rows.

Cephalic hood exposed, short, margin finely papillose. Anterior end everted, previously removed, not available. Cephalic cage chaetae about as long as 3 times body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short series, each about the body corners, six noto- and four neurochaetae per bundle.

Anterior dorsal margin of first chaetiger with a large, bifid projection; chaetigers 1-4 with low notopodial lobes. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage chaetae to body chaetae gradual; short bidentate neurohooks start in chaetiger 10. Gonopodial lobes not seen.

Parapodia better developed in anterior chaetigers; posterior ones reduced, placed over the body corners. Median neuropodia ventrolateral. Notopodia short, conical lobes, with mostly two large postchaetal papillae. Neuropodia low transverse lobe, with one postchaetal papilla.

Median notochaetae arranged in short transverse series, 5-6 per bundle, as long as body width; all multiarticulated capillaries, each with short articles basally, long medially and distally (Fig. 10E, insert). Short bidentate multiarticulated neurohooks from chaetiger 10, arranged in a transverse or oblique series, 3-4 anteriorly, 4-5 in median chaetigers. Anchylosed bidentate neurohooks starting by chaetiger 30 (Fig. 10F); by chaetiger 40 multiarticulate neurohooks completely replaced by anchylosed ones. Multiarticulated neurohooks with short articles basally, longer medially, short subdistally. Anchylosed neurohooks bidentate, with short articles basally and medially, fading subdistally, subdistally slightly expanded; blade transparent, main fang curved, especially in multiarticulated hooks (Fig. 10F, inserts), accessory tooth thin, widening distally.

Posterior end unknown.

REMARKS

Trophoniella fauveli n. sp. is closely allied to *T. capitata* n. comb. because both species have large, sparse sediment particles on dorsal and often lateral surfaces, and anchylosed neurohooks from median chaetigers. They especially differ regarding the presence of notopodial lobes and on the start of anchylosed neurohooks; thus, *T. fauveli* n. sp. has notopodial lobes and anchylosed neurohooks from chaetiger 40, whereas *T. capitata* n. comb. lacks notopodial lobes and its anchylosed neurohooks start by chaetiger 28.

On the other hand, because of the presence of large, scarce, sediment particles over the few anterior chaetigers, it resembles the illustrations made by Savigny (1822) for his *Aristenia conspurcata.* However, as it has been stated elsewhere (Salazar-Vallejo 2011a), the lack of chaetal details, especially for those present in posterior chaetigers, has resulted in it being regarded as indeterminable. It is noteworthy that this newly described species was also collected in Egypt, although perhaps in different depths. Without the critical missing information, the status of *A. conspurcata* cannot be modified.

Trophoniella fernandensis
(Augener, 1918) reinstated, n. comb.
(Fig. 11)

Pycnoderma fernandense Augener, 1918: 448-451, pl. 6, figs 148, 182, pl. 7, figs 237, 238, textfig. 67.

Flabelligera affinis – Fauvel & Rullier 1959: 180 (*non* Sars 1829).

Piromis arenosus – Fauvel & Rullier 1959: 181. — Intes & Le Lœuff 1977: 236 (*non* Kinberg 1867).

MATERIAL EXAMINED. — **Mediterranean Sea.** Anterior fragment (IRFA), off Rovigno d'Istria, Croatia, stn 314 (no further data), 1966, Vatova (18 mm long, 2.3 mm wide, cephalic cage chaetae broken, 34 chaetigers). — 1 specimen (SMF 14849), baie du Lazaret, Toulon, France, 1.VI.1982, V. Díaz-Castañeda (23.5 mm long, 1.5 mm wide, cephalic cage 1.5 mm long, 59 chaetigers; regenerating the dorsal body wall of first few chaetigers; first anchylosed neurohooks by chaetiger 32); 1 specimen and 3 fragments (SMF 14904), same data, but 28.VI.1982 (complete 9.0 mm long, 1.0 mm wide, cephalic cage 1.0 mm long, 49 chaetigers); 1 mature ♀ (SMF 14937), broken in 2, many chaetae broken, same data, but 11.III.1983 (20 mm long, 1.8 mm wide, cephalic cage 2 mm long, 56 chaetigers; oocytes about 100 µm); 1 specimen (SMF 14993), same data, but 12.X.1982 (used for redescription); 2 specimens (SMF 15124) damaged, many chaetae broken, same data, but 15.XI.1982 (11.8-20.0 mm long, 1-2 mm wide, cephalic cage 0-2 mm long, 39-52 chaetigers); anterior fragment (SMF 15054), damaged, most chaetae broken, same data, but 11.III.1983 (17 mm long, 1.0 mm wide, cephalic cage broken, 39 chaetigers); 2 fragments (SMF 15136), same data, but 15.XI.1982. — Anterior fragment (USNM 1156916), collected off île de Ryon, S of Marseille, France, dredged, 60-80 m, 1969-1970, M. Pichon (24 mm long, 2.5 mm wide, cephalic cage chaetae 2 mm long, 45 chaetigers).

Eastern tropical Atlantic. Anterior fragment (MNHN A383), off Conakry, Guinea, R/V *Calypso*, stn 7 (09°40'N, 14°05'W), 18 m, 17.V.1956 (apparently complete, tapered anteriorly, 20 mm long, 2 mm wide, cephalic cage chaetae 2 mm, 37 chaetigers). — Anterior fragment (MNHN A383), off Sekondi-Takoradi, Ghana, R/V *Calypso*, stn 26 (04°37'N, 00°50'W), 90-100 m, 24.V.1956 (without posterior region; red-yellowish, tapered anteriorly, 21 mm long, 2 mm wide, cephalic cage chaetae 2 mm, 45 chaetigers).

Red Sea. Anterior fragment (BMNH 1955.10.12.49), complete, with an anterodorsal dissection and a lateral distortion due to pressure, off Arlit (31°41'14"N, 34°56'18"E), Israel, dredged, 36 m, 2.XII.1948, A. Yashouv (12.5 mm long, 1.8 mm wide, cephalic

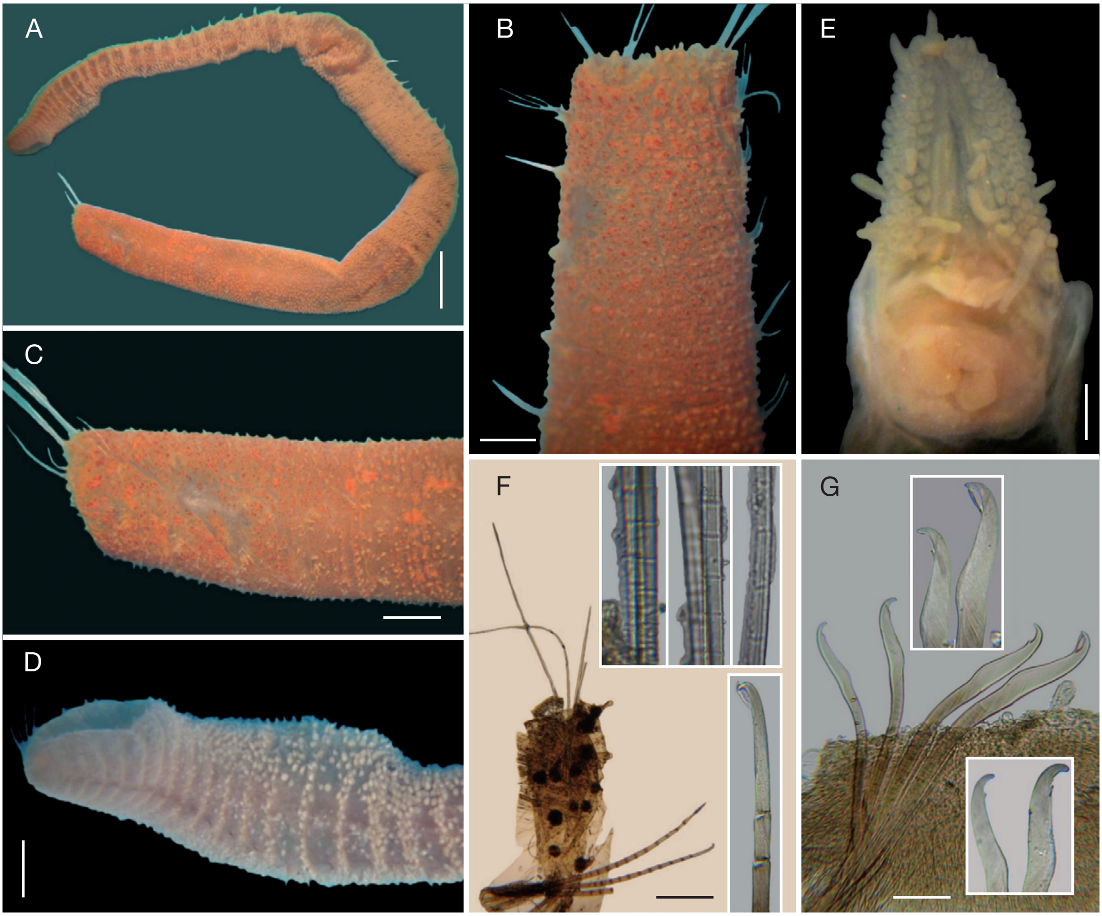

FIG. 11. — *Trophoniella fernandensis* (Augener, 1918) reinstated, n. comb.: **A**, complete specimen (SMF 14993), lateral view; **B**, same, anterior end, dorsal view; **C**, same, anterior end, lateral view; **D**, same, posterior region, lateral view; **E**, another specimen (SMF 14937), head, frontal view, palps and most branchiae detached; **F**, previous specimen (SMF 14993), chaetiger 9 complete (inserts: basal, medial and distal notochaetal regions and neurochaetal tip); **G**, same, chaetiger 56, neurochaetae (inserts: neurochaetal tips). Scale bars: A, 2 mm; B, 0.85 mm; C, 1.5 mm; D, 0.4 mm; E, 0.2 mm; F, 210 µm; G, 90 µm.

cage 1.5 mm long, 34 chaetigers; median chaetigers with 13-15 transverse rows of papillae).

DISTRIBUTION. — Originally described from equatorial western Africa, it apparently ranges northwards into the Mediterranean and probably into the Red Sea, in soft bottoms in 25-70 m depth. This distribution might include more than one species, but they have been retained as a single one because of the preservation condition of the materials. There seems to be differences in the relative size of articles in notochaetae, being shorter in western African specimens and medium-sized or long in Mediterranean ones, but to separate them as distinct species requires better specimens.

ETYMOLOGY. — The original epithet spelling, "fernandense", might have tried to indicate one of the collecting sites (Fernando Póo Island, Guinea), adjusted to the apparent feminine gender of *Pycnoderma* Grube, 1877. The suffix has been corrected to *-ensis*, as a means to indicate that the species thrives in that locality.

DESCRIPTION

Complete specimen (SMF 14993), most chaetae broken, some papillae eroded (Fig. 11A). Body subcylindrical, truncate anteriorly, tapering posteriorly; body colour concentrated in papillae; reddish anteriorly, fading to orange medially, pale posteriorly, 32 mm long, 2.5 mm wide, cephalic cage chaetae broken, 2 mm long, 63 chaetigers. Tunic thin, without sediment particles, softer in posterior chaetigers, not forming a crust. Papillae small, dorsal papillae slightly larger than ventral ones, each with fine brown-reddish sediment forming brown spherules, arranged in about 15 transverse rows in median segments.

Anterior end observed in two other specimens (MNHN A383, SMF 14937; Fig. 11E). Prostomium low cone; eyes dark brown, medium-sized. Caruncle long, separating the branchial plate in two lateral groups, not reaching the posterior margin. Palps long, pale; palp keels rounded, elevated. Lateral, ventral and dorsal lips apparently fused, forming a projected cone. Branchiae thin, cirriform, motled with irregular brown bands or colourless; sessile on a tongue-like protuberance, separated in two lateral groups; each group with branchiae arranged in four concentric rows, longest row with up to 20 filaments, about 60 filaments per group. Largest branchiae thinner and as long as palps. Nephridial lobes not seen.

Cephalic cage made by chaetiger 1 (Fig. 11B, C), chaetae less than $^{1}/_{15}$ body length or slightly shorter than body width; each chaeta thin, about 2 mm long (slightly less than body width at chaetiger 10); 4-5 chaetae per bundle. Chaetal transition abrupt, chaetiger 2 with shorter notochaetae (1 mm long) and bifid neurochaetae. First chaetigers without dorsal lobes nor larger middorsal papillae. Dorsal margin of chaetiger 1 papillated. Ventral surface without ventrolateral lappets or gonopodial lobes.

Noto- and neuropodia lateral, both scarcely developed (Fig. 11F); associated papillae not markedly longer than other dorsal ones.

Median notochaetae arranged in longitudinal or oblique series, 4-5 notochaetae anteriorly, 5-7 posteriorly, as long as ½ body width; all notochaetae multiarticulated capillaries with long articles throughout the chaeta (Fig. 11F, inserts), shorter in other specimens. Neuropodia scarcely developed; associated papillae not markedly longer than the dorsal ones; 3-4 bidentate hooks anteriorly, 2-3 posteriorly. Bidentate neurohooks starting from chaetiger 2 (IRFA; in other specimens mostly broken), with short articles basally, longer ones medially and distally, continued to posterior chaetigers; from about chaetiger 45 anchylosed neurohooks, continued to the posterior end, bidentate, medially expanded, with short rings basally, fang curved, accessory tooth laminar, subdistally markedly expanded, fragile, often reduced to a thin, triangular blade (Fig. 11G, inserts).

Posterior end slightly swollen, without achaetous segments (Fig. 11D); pygidium rounded, anus terminal, without anal cirri.

Remarks

Trophoniella fernandensis n. comb. resembles *T. fiegei* n. sp. but they differ in the tunic surface, number of transverse rows of papillae and the start of anchylosed neurohooks. In *T. fernandensis* n. comb. the tunic is velvety or rugose, whereas it is smooth in *T. fiegei* n. sp.; there are 15 transverse rows of papillae in *T. fernandensis* n. comb. whereas there are only 6-9 in *T. fiegei* n. sp., and in *T. fernandensis* n. comb. anchylosed neurohooks start by chaetiger 45 whereas they start by chaetiger 50 in *T. fiegei* n. sp.

Another species, *Pycnoderma glabra* (Treadwell, 1901), is regretfully too poorly known and has been included in that genus because there were no posterior chaetae (Salazar-Vallejo 2011a: 38), but that transfer might be modified once more and better specimens will be available. In case they belong to the same genus, their body papillae are homogeneously short and not adhering large sediment grains. These two species might be similar and besides the type of posterior neurochaetae, the only apparent differences are the amount of transverse rows of papillae in median chaetigers and the formation of a crust in posterior chaetigers; thus, in *T. fernandensis* n. comb., median chaetigers have about 15 transverse rows per segment and its tunic does not form a crust, whereas in *P. glabra* there are only about 10 transverse rows per segment and its tunic makes a crust in posterior chaetigers. This difference, however, requires more specimens of the latter species to better define its diagnostic features and its generic placement.

As originally stated by Augener (1918: 451, 452), his species is more closely allied to other species formerly belonging in *Piromis*, rather than in *Pycnoderma*; he may have assigned his species to that genus because it lacks any large sediment

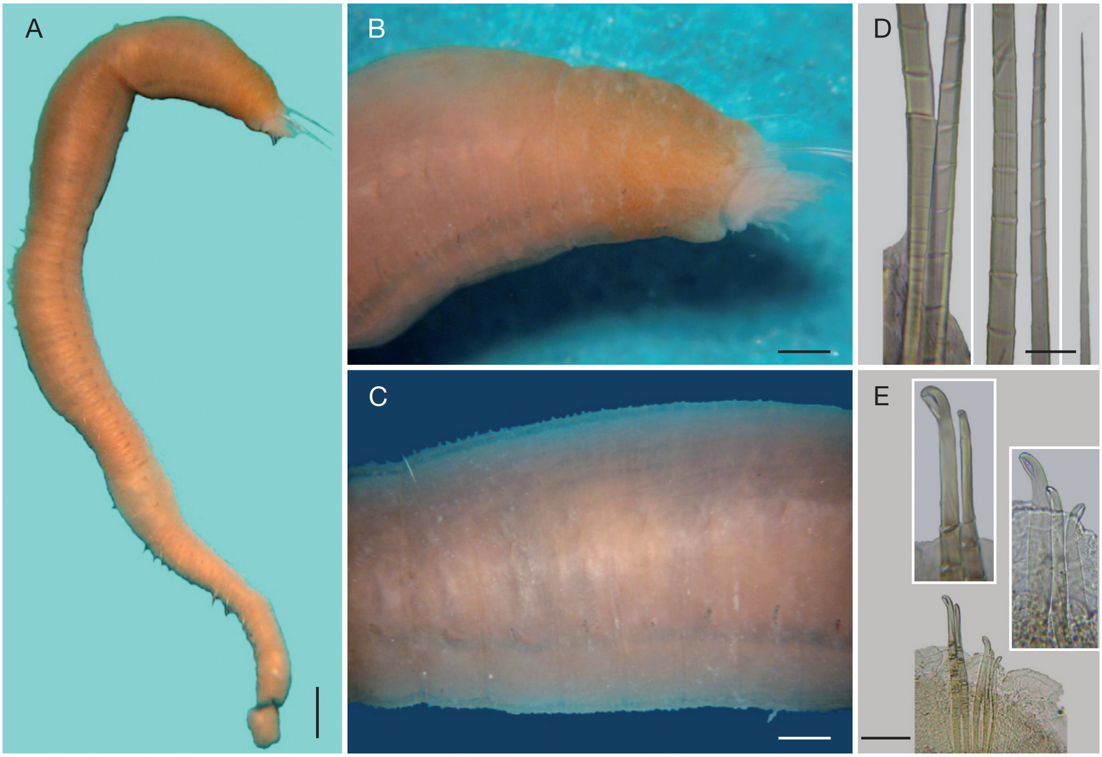

FIG. 12. — *Trophoniella fiegei* n. sp. holotype (SMF 15379): **A**, lateral view; **B**, anterior end, lateral view; **C**, anterior chaetigers; **D**, far posterior chaetiger, notochaetal basal, medial and distal regions; **E**, same chaetiger, neurochaetae (inserts: neurochaetal tips). Scale bars: A, 1.6 mm; B, 0.5 mm; C, 0.4 mm; D, 28 µm; E, 90 µm.

particle adhered to the outer cover, just as it happens in the then only known species, *P. congoense* Grube, 1877. However, it shares chaetal features with *Trophoniella*, especially by the presence of anchylosed neurohooks in the posterior fourth of the body, which were even detailed in the original description, hence the new combination.

Trophoniella fiegei n. sp.
(Fig. 12)

TYPE MATERIAL. — **Persian Gulf.** Holotype (SMF 15379), off Jebel Ali, Dubai, low intertidal, 19.III.1998, M. Apel.

ADDITIONAL MATERIAL. — **Gulf of Oman, Arabian Sea.** 3 anterior fragments (LACM-AHF 2483), International Indian Ocean expedition, Iran, off Chan Bahar Bay, R/V *Anton Bruun*, stn AB 247B (25°06'N, 60°45'E), 110 m, sticky clay with shells, 28.XI.1963 (larger fragment regenerating the anterior end, 17.5 mm long, 2.5 mm wide, cephalic cage damaged, 2 mm long, 32 chaetigers; gonopodial papillae pale, low lobes in chaetiger 5).

TYPE LOCALITY. — Jebel Ali, Dubai, low intertidal.

DISTRIBUTION. — Persian Gulf and Gulf of Oman, from low intertidal to 110 m depth.

ETYMOLOGY. — This species is named after Dr Dieter Fiege, friend, curator and polychaete specialist from the SMF, in recognition for his fine publications on polychaete taxonomy, because he has been very helpful during my research activities, and by preparing a large loan of specimens from the Indian Ocean, including the specimen for this description.

DESCRIPTION

Holotype (SMF 15379) subcylindrical, thin, wider anteriorly, tapering towards both ends (Fig. 12A).

Body yellowish, slightly darker anteriorly, complete, posterior end detached, most chaetae broken, some papillae eroded, 25 mm long, 2.5 mm wide, cephalic cage chaetae 2 mm long, 60 + 3 chaetigers. Tunic thick, smooth, without sediment particles. Papillae small, sparse; dorsal papillae slightly larger than ventral ones, all capitate, arranged in 6-9 transversal rows per segment in median chaetigers (Fig. 12B, C).

Anterior end partially exposed (Fig. 12B); not dissected to avoid further damage. Cephalic hood partially exposed, margin papillose. Palps lost. Branchiae thin, pale, with irregular dark blotches. Other features not observed.

Cephalic cage chaetae less than ⅒ body length or slightly shorter than body width; chaetiger 1 involved in the cephalic cage, three noto- and two neurochaetae per side. Chaetal transition gradual, chaetiger 6 with shorter neurochaetae each with long articles. First chaetigers without dorsal lobes nor large, middorsal papillae. Chaetigers 1-3 of about the same length. Gonopodial lobes not seen.

Parapodia poorly developed, lateral; median neuropodia ventrolateral. Noto- and neuropodia lateral. Notopodia scarcely developed; associated papillae slightly larger than other dorsal ones.

Median notochaetae arranged in short oblique series, 4-5 notochaetae anteriorly, 5-6 posteriorly, as long as ½-⅓ body width; all notochaetae multiarticulated capillaries, each with long articles throughout the chaeta (Fig. 12D). Neuropodia scarcely developed; associated papillae slightly larger than other lateral ones. Multiarticulated capillaries with short articles basally, medium-sized medially and distally in chaetigers 1-5. From chaetiger 6, shorter multiarticulated neurohooks, arranged in a short transverse series, each with four hooks medially, five posteriorly. Each hook with short articles basally, long articles medially and distally; tips falcate, bidentate. Anchylosed neurohooks bidentate, from chaetiger 50 (Fig. 12E), each pale, with short rings basally, subdistally straight, tapering to the fang and accessory tooth, both of about the same length.

Posterior end without achaetous segments; pygidium with anus terminal with a middorsal thick lobe, slightly eroded.

REMARKS

Trophoniella fiegei n. sp. belongs to the group of species lacking sediment particles on the tunic and having a finely papillated surface such as *T. fernandensis* n. comb. from western Africa and the Mediterranean Sea. The main difference between these species is the relative number of transverse rows of papillae; thus, *T. fiegei* n. sp. has 6-7 rows, whereas there are about 15 rows in *T. fernandensis* n. comb.

Trophoniella grandis
(Blanchard *in* Gay, 1849) n. comb.
(Fig. 13)

Siphostoma grande Blanchard *in* Gay, 1849: 35, 36. — Rozbaczylo 1985: 161.

Lophiocephala grandis – Quatrefages 1866: 485.

Stylarioides (*Trophonia*) *capensis* – Gravier 1909: 649, 650, pl. 18, figs 58, 59; 1910: C116, 117, pl. 10, figs 62, 63 (*non* McIntosh 1885).

Stylarioides capensis americana Monro, 1928: 96, 97, fig. 16; 1933: 1057, 1058, textfig. 6A, B *partim*.

TYPE MATERIAL. — **Eastern Pacific Ocean**. 2 syntypes of *Siphostoma grande*, larger syntype (MNHN 378), well preserved, smaller syntype (MNHN 379), dried out, Coquimbo (29°57'11"S, 71°20'36"W), Chile, Gaudichaud (smaller syntype 104 mm long, 4 mm wide, cephalic cage 9 mm long, 178 chaetigers; first neurohooks in chaetiger 7, dorsal lobes in chaetigers 2-7). — 1 syntype of *S. c. americana* (BMNH 1933.7.10.140), damaged, dorsally dissected, off Balboa, Panama, 1923/4, C. Crossland (12.5 mm long, 2 mm wide, cephalic cage 4 mm long, 49 chaetigers, first neurohooks from chaetiger 5; sediment cover previously removed); 1 syntype of *S. c. americana* (BMNH 1933.7.10.141), damaged, dorsally dissected, broken in 2 pieces, off Balboa, Panama, 1923/4, C. Crossland (15 mm long, 1 mm wide, cephalic cage 4.5 mm long, 50 chaetigers, first neurohooks from chaetiger 5; sediment cover previously removed).

ADDITIONAL MATERIAL. — **Eastern Pacific Ocean.** 1 mature ♀ (CAS 168314), International Galápagos Scientific Project, southwest coast of Isla Pinta (Abingdon Island), Galápagos, tide pools, 25.V.1964, D. Q. Cavagnaro (48 mm long, 5 mm wide, cephalic cage chaetae 10 mm long; 68 chaetigers; first neurohooks from chaetiger 6; oocytes about 100 µm in diameter).

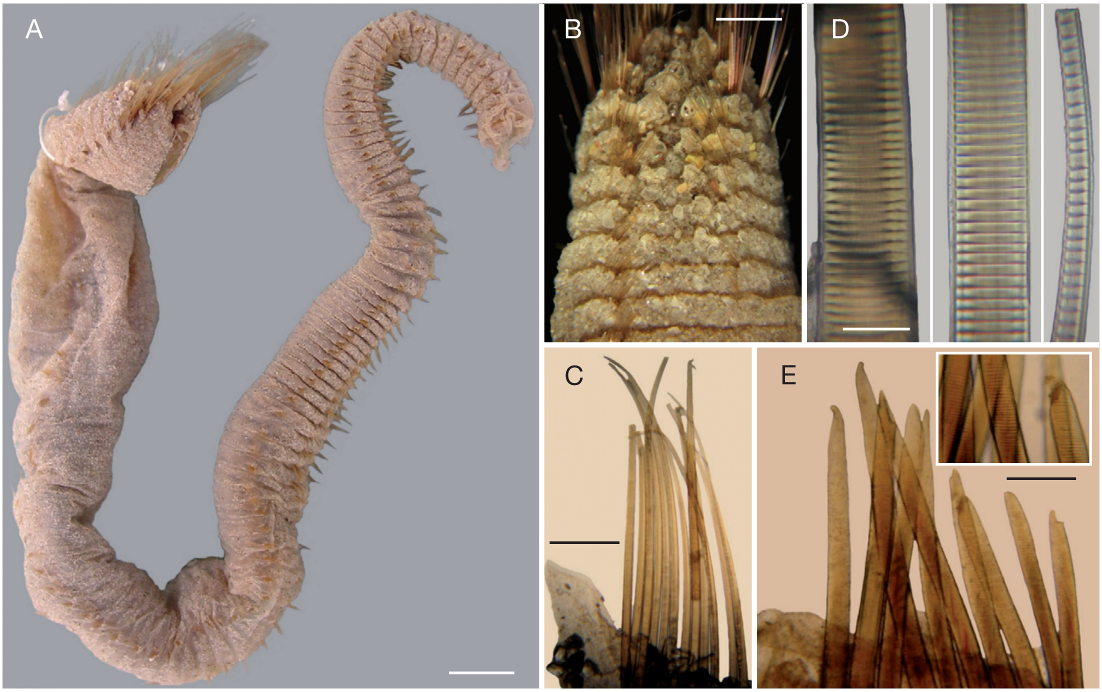

FIG. 13. — *Trophoniella grandis* (Blanchard *in* Gay, 1849) n. comb., largest syntype (MNHN 378): **A**, lateral view; **B**, anterior end, dorsal view; **C**, notopodium from chaetiger 35; **D**, notochaetal basal, medial and distal regions; **E**, neurohooks from chaetiger 76 (insert: enlargement to show anchylosed articles). Scale bars: A, 5 mm; B, 2.9 mm; C, 0.4 mm; D, 45 µm; E, 180 µm.

DISTRIBUTION. — From the Galápagos Islands to the Tumbes Peninsula (Talcahuano, Concepción), Chile. Fauchald (1972: 414) erroneously listed Tumbes, Peru, as the type locality.

DESCRIPTION

Larger syntype of *S. grandis* (MNHN 378) grayish, posteriorly incomplete (Fig. 13A), soft, preserved in alcohol. Body fusiform, cylindrical, tapering posteriorly, 142 mm long, 10 mm wide, cephalic cage 10 mm long, 105 chaetigers. Tunic completely covered by a fine layer of fine sediment particles, less extended ventrally, especially in posterior chaetigers (smaller syntype with large sediment particles dorsally, smaller particles ventrally). Body papillated, pale, body wall pale (black in smaller syntype). Papillae mostly collapsed, ventrally arranged in four longitudinal rows or double papillar scars. Dorsal lobes in chaetigers 2-8.

Anterior end not exposed; not dissected to avoid further damage. Cephalic cage chaetae as long as body width. Chaetigers 1-4 involved in the cephalic cage; chaetae arranged as short dorsolateral series. Chaetiger 1 with 12-16 noto- and 10 neurochaetae, chaetiger 2 with 10 chaetae per bundle, chaetiger 3 with 10 chaetae per bundle, chaetiger 4 with nine noto- and eight neurochaetae. Anterior dorsal margin of first chaetiger with a short, conical, papillated, bifid lobe, directed ventrally. Chaetigers 2-8 with two large, dorsal papillae per segment, decreasing in size posteriorly, each as a rounded lobe, directed anteriorly (Fig. 13B). Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt; short, dark, anchylosed neurohooks starting in chaetiger 7. Gonopodial lobes not seen (BMNH 1933.7.10.140 with nephridial papillae long, in the external surface of branchial plate).

Parapodia poorly developed, chaetae emerge from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia short, transverse slits; notopodia with two postchaetal papillae, neuropodia with three smaller postchaetal papillae. Noto- and neuropodia distant to each other.

Median notochaetae arranged in short transverse series, 11-12 per bundle, as long as ¼-⅕ body width (Fig. 13C); all notochaetae multiarticulated capillaries, mostly broken distally, each with short articles, becoming slightly longer distally (Fig. 13D), tips falcate, hyaline. Neurochaetae multiarticulated capillaries in chaetigers 1-6; straight, anchylosed neurohooks from chaetiger 7, arranged in transverse series, 7-9 per bundle (Fig. 13E). Each hook dark brown, with short rings continued to the subdistal, slightly expanded region, blade less pigmented, finely obliquely striated, distally entire, falcate, surface rough with adsorbed materials.

Posterior end (in smaller syntype) tapering to a blunt cone; pygidium with anus terminal, without anal cirri.

Variation

There are several features that show certain size-dependency, especially the number of chaetae per bundle and the number of anterior segments with dorsal tubercles. The variation is limited, however, and under a certain range of variation, they can be employed to separate similar species having a relatively similar size. On the other hand, the start of neurohooks is consistent.

REMARKS

Trophoniella grandis n. comb. was described as *Siphostoma grande* in a major work on Chilean natural history involving several French scientists. However, Quatrefages (1866) did not acknowledge this; in fact, he had already employed the "Nob." abbreviation before (Quatrefages 1849). This comes from the Latin word "nobis", meaning "to us" and it is equivalent to "mihi", which means, in turn, "to me […] and used after a name to indicate the author's responsibility for it" (Stearn 1992). Thus, he introduced new names even when he was aware that a previous name had already been used for the same species (cf. Quatrefages 1866: 476 under *Chloraema dubium* as a new name, instead of *Flabelligera* (*olim Siphostoma*) *diplochaitus* Otto, 1821). Therefore, because both names have been introduced for Chilean flabelligerids, in both cases the same epithet was employed, and because collecting trips to Chile was not frequent, both names must have the same type specimen, consequently become objective synonyms, and Blanchard's name has priority. It must be stated that Quatrefages noticed the apparent lack of notochaetae in several anterior chaetigers, and this would explain why he moved the species to *Lophiocephala* Costa, which is a junior synonym of *Stylarioides* (Salazar-Vallejo 2011b). The specimen was distorted during preservation; most of the tunic was detached from the body wall, and especially in anterior chaetigers, chaetae can be seen by transparency under the loose tunic, or the aligned chaetal scars can be seen in the corresponding sites.

Trophoniella grandis n. comb. resembles *T. ehlersi* n. comb. because their tunics include fine sediment particles over the dorsal and ventral surfaces. They differ because in *T. grandis* n. comb. there are dorsal tubercles in the first few chaetigers, whereas in *T. ehlersi* n. comb. the anterior chaetigers do not have dorsal tubercles or notopodial lobes, and because in *T. grandis* n. comb. the falcate neurohooks start by chaetiger 7 whereas they start by chaetiger 5 in *T. ehlersi* n. comb.

Trophoniella harrisae n. sp.
(Fig. 14)

Piromis hospitis – Blake 2000: 12, 13, fig. 1.4 (*non* Fauchald 1972).

TYPE MATERIAL. — **Northeastern Pacific Ocean, California.** Holotype (LACM-AHF 2486), off White Point, R/V *Velero IV*, stn not in log book, 93 m, 10.IV.1957. Paratypes: 3 anterior fragments and some posterior ones (LACM-AHF 2487), 2 miles off Point Fermin Light, R/V *Velero IV*, stn 5502 (33°41'30"N, 118°19'50"W), 49 fathoms, fine, gray, silty sand, 16.XII.1957 (15-50 mm long, 3.5-8.0 mm wide, cephalic cage 6-7 mm long, 28-53 chaetigers, dorsal tubercles in chaetigers 2-end of fragment; first neurohooks from chaetigers 22-27). — 2 complete and another one almost complete specimens (LACM-AHF 2488), 3.7 miles off San Clemente Pier, R/V *Velero IV*, stn 5632 (33°22'50"N, 117°39'00"W), 32 fathoms (tag: 213 feet), fine green sand, 22.II.1958 (completes 75-76 mm long, 6-7 mm wide, cephalic cage 5.5-6.0 mm long, 96-107 chaetigers, dorsal tubercles in

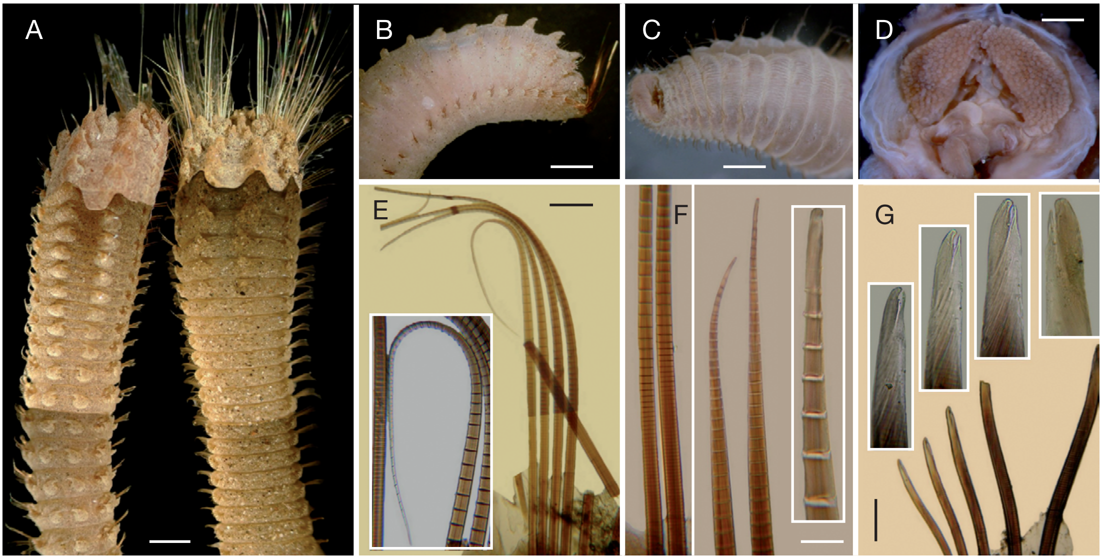

FIG. 14. — *Trophoniella harrisae* n. sp.: **A**, holotypes of *T. harrisae* n. sp. (left, LACM-AHF 2486) and *T. hospita* (Fauchald, 1972) n. comb. (right, LACM-AHF 1178), dorsal view; **B**, paratype of *T. harrisae* n. sp. (LACM-AHF 2488), anterior end, lateral view; **C**, paratype (LACM-AHF 2490), posterior end, lateral view; **D**, same, head dissected; palps and branchiae detached; **E**, paratype (LACM-AHF 2478), chaetiger 13, notochaetae (insert: basal, medial and distal regions); **F**, same, chaetiger 10, neurochaetae (insert: chaetal tip); **G**, same, chaetiger 27, neurochaetae (inserts: chaetal tips). Scale bars: A, 3.8 mm; B, 2.6 mm; C, 0.7 mm; D, 0.8 mm; E, 180 µm; F, 150 µm; G, 160 µm.

chaetigers 2-90 [95]; first neurohooks from chaetigers 27-28; the other 63 mm long, 7 mm wide, cephalic cage 7 mm long, 86 chaetigers, dorsal tubercles in chaetigers 2-85; first neurohooks from chaetiger 24). — 1 anterior fragment (LACM-AHF 2489), 2.75 miles off Point Fermin Light, R/V *Velero IV*, stn 5664 (33°43'10"N, 118°20'40"W), 11 fathoms, medium gray to black sand, 21.III.1958 (58 mm long, 6 mm wide, cephalic cage 6.5 mm long, 64 chaetigers, dorsal tubercles in chaetigers 2-37 [tunic removed from dorsum of chaetiger 38]; first neurohooks from chaetiger 20). — 2 anterior fragments (LACM-AHF 2490), 10.3 miles off Santa Monica Pier Light, R/V *Velero IV*, stn 5975 (34°00'28"N, 118°42'28"W), 29 fathoms, green mud, 22.XI.1958 (largest dissected; 51 mm long, 7 mm wide, cephalic cage 5 mm long, 43 chaetigers; dorsal lappets in chaetigers 2-43; first neurohooks from chaetiger 25).

ADDITIONAL MATERIAL. — **Northeastern Pacific Ocean, California.** Anterior fragment (CAS 133248), Moss Landing Monterey Bay Study, 36°52.3'N, 121°59.8'W, 63 m, 13.X.1971. — Anterior fragment (CAS 133251), Moss Landing Monterey Bay Study, 36°50.8'N, 121°53.6'W, 62.5 m, 24.XI.1971.

TYPE LOCALITY. — Off White Point, California, in sediments at 93 m depth.

DISTRIBUTION. — Central to southern California sediments in 22-100 m depth.

ETYMOLOGY. — This species is gratefully being named after Leslie H. Harris, who has worked a lot on Californian polychaete fauna, have supported my research activities during many years, and especially because she noticed that there were some relevant differences between this and similar species, paving the road for this description.

DESCRIPTION

Holotype complete, brownish pink (Fig. 14A), broken into two pieces, most chaetae broken; body club-shaped, tapering posteriorly, 147 mm long, 10 mm wide, cephalic cage 9 mm long, 141 chaetigers. Tunic papillated, with fine sediment particles dorsally, almost no sediment particles ventrally; posterior region almost without sediment (Fig. 14C). Papillae arranged in longitudinal rows, two dorsal series of larger papillae, four ventral ones with smaller papillae. Dorsal papillae forming large, mammiliform, paired dorsal tubercles, decreasing in size posteriorly, present to chaetiger 40.

Anterior end dissected from one paratype (LACM-AHF 2490). Cephalic hood not exposed, smooth. Prostomium low, eyes blackish, large. Caruncle well developed, running through the tongue-like branchial plate, but not reaching the distal margin, lateral ridges black. Palps black, deeply corrugated; palp keels rounded, slightly pigmented. Lips black; lateral and ventral lips fused, retracted; dorsal lip projected as a small rounded lobe. Branchiae cirriform, pale, sessile on a short, tongue-like protuberance, separated in two lateral groups, each with filaments arranged in about 12 concentric rows, over 100 filaments per group (Fig. 14D). Branchiae slightly shorter than palps. Nephridial lobes double, dehiscent, stemming from the basal inner corner of branchial groups.

Cephalic cage chaetae about $\frac{1}{15}$ body length, or about as long as body width (Fig. 14B). Chaetigers 1-3 involved in the cephalic cage (damaged); chaetae arranged in short series, chaetiger 1 dorsolateral, chaetigers 2-3 lateral. Chaetiger 1 with about 12 noto- and 10 neurochaetae, chaetigers 2-3 with about six noto- and eight neurochaetae each. Anterior dorsal margin of first chaetiger with a median multifid lobe, projected anteriorly. Anterior chaetigers with long, notopodial papillae. Chaetigers 1-3 progressively longer. Chaetal transition from cephalic cage to body chaetae abrupt; bidentate neurohooks present from chaetiger 5, each with short articles basally, medium-sized articles medially and distally; by chaetiger 20 anchylosed, bidentate neurohooks. Gonopodial lobes not seen.

Parapodia poorly developed; chaetigers 1-9 with large, globose notopodial lobe, decreasing posteriorly; in others, chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia with one small prechaetal papilla and three larger postchaetal papillae. Noto- and neuropodia distant to each other.

Median notochaetae arranged in short transverse series; 8-9 per bundle, as long as ¼ body width (after the swollen anterior region); all notochaetae multiarticulated capillaries, each with short articles basally, medium-sized medially, longer distally (Fig. 14E). Neurochaetae multiarticulated capillaries in chaetigers 1-4. Bidentate neurohooks with medium-sized articles in chaetigers 5-19 (Fig. 14F), being gradually replaced by anchylosed bidentate neurohooks, arranged in an oblique series, each with five per bundle (Fig. 14G); each neurohook with short rings continued to the subdistal straight region, blade bifid, main fang and accessory tooth almost parallel, accessory tooth thinner, sharper, shorter.

Posterior region almost without sediment particles (Fig. 14C), tapering to a blunt cone; pygidium with large anus, as wide as pygidium, without anal cirri.

REMARKS

Trophoniella harrisae n. sp. resembles *T. hospita* n. comb. and *T. orensanzi* n. sp. because of the presence of large dorsal lappets along anterior chaetigers. They differ because in *T. harrisae* n. sp. the dorsal tubercles extend along about 40 chaetigers, whereas in *T. hospita* n. comb. they extend along about 25 chaetigers, and only along 10 chaetigers in *T. orensanzi* n. sp. Most of the specimens examined were previously identified as *Piromis capulata* (Moore, 1909); they differ from *P. capulata*, which is an intertidal and shallow-water form, in the type of neurochaetae which separates them in different genera, and about the development of paired dorsal lappets which is much reduced in *P. capulata* (see Salazar-Vallejo 2011a: 14).

Trophoniella havaica (Kinberg, 1867) n. comb.
(Fig. 15)

Chloraema havaica Kinberg, 1867: 337, 338; 1910: 68, pl. 26, fig. 1.

Stylarioides havaica – Hartman 1949: 118, pl. 15, figs 5, 6.

Pherusa havaica – Hartman 1966: 228. — Bailey-Brock & Hartman 1987: 392, fig. 3.2.167.

TYPE MATERIAL. — **North Pacific Ocean**. Holotype (SMNH 508), R/V *Eugenie* expedition, 1851-1853, Oahu (21°19'N, 157°52'W), Honolulu, Hawaii, no further data.

DISTRIBUTION. — The species has been found only in the type locality, Oahu, Hawaii.

DESCRIPTION

Holotype broken in three pieces, anterior and posterior ends and a median segment (Fig. 15A).

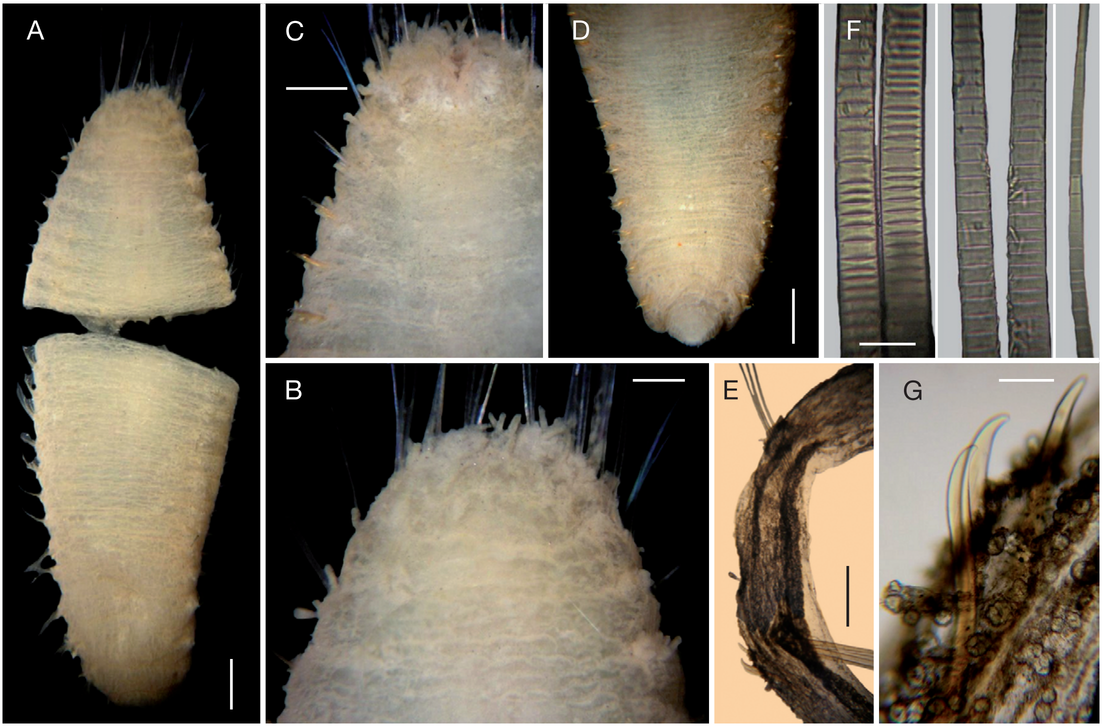

FIG. 15. — *Trophoniella havaica* (Kinberg, 1867) n. comb., holotype (SMNH 508): **A**, anterior and posterior fragments, dorsal view; **B**, anterior end, dorsal view; **C**, anterior end, ventral view; **D**, posterior end, ventral view; **E**, parapodium from median chaetiger; **F**, same, notochaetal basal, medial and distal regions; **G**, same, neurohooks. Scale bars: A, 1 mm; B, 0.4 mm; C, 0.33 mm; D, 0.8 mm; E, 0.5 mm; F, 30 µm; G, 90 µm.

Body fusiform, tapering posteriorly. Anterior fragment 5 mm long, 5 mm wide, cephalic cage 3 mm long, nine chaetigers; posterior fragment 8 mm long, 5 mm wide, 19 chaetigers (last five in regeneration). Tunic thick, finely papillated, without sediment particles. Papillae abundant, most thin, fragile, capitate or digitate; larger papillae clavate, placed along chaetal lobes and arranged in longitudinal rows, two dorsal, one lateral and four ventral ones.

Anterior end not exposed; not dissected to avoid further damage. Cephalic cage chaetae as long as ¾ body width. Chaetigers 1-3 involved in the cephalic cage, chaetae arranged in short series with 3-4 noto- and 3-4 neurochaetae. Anterior dorsal margin of first chaetiger with a trifid lobe, breaking apart, tines twisted (Fig. 15B). Anterior chaetigers with long papillae. Chaetigers 1-3 progressively longer. Chaetal transition from cephalic cage chaetae to body chaetae abrupt, falcate anchylosed neurohooks starting in chaetiger 5 (Fig. 15C). Gonopodial lobes not visible.

Parapodia lateral, poorly developed; chaetae emerging from the body wall (Fig. 15E). Median neuropodia ventrolateral. Noto- and neuropodia not forming long lobes; anterior parapodia with few longer papillae. Median notopodia with 2-3 infrachaetal smaller papillae and one large median chaetal lobe papilla, sometimes missing, each markedly expanded distally. Neuropodia with 1-2 infrachaetal and 1-2 suprachaetal papillae.

Median notochaetae arranged in short transverse series; 4-5 notochaetae per bundle, about as long as ⅕ body width; all notochaetae multiarticulated capillaries, each with articles short basally and medially, long distally, but not in a regular pattern, a longer article being placed between a series of smaller ones

(Fig. 15F). Neurochaetae multiarticulated capillaries in chaetigers 1-4, all articles short, tips eroded. Anchylosed, darker neurohooks from chaetiger 5, arranged in transverse series (oblique in posterior chaetigers), 3-4 in anterior and 4-5 in posterior chaetigers, barely exposed, feebly developed rings basally, not visible in the exposed part, subdistally straight, fang curved, entire (Fig. 15G).

Posterior end regenerating, tapered to a blunt round tip (Fig. 15D), with a middorsal longitudinal furrow; pygidium with anus terminal, without anal cirri.

REMARKS

Trophoniella havaica n. comb. resembles other species having anchylosed neurohooks from an anterior chaetiger and lacking sediment particles on the body, such as *T. minuta* n. comb., and two newly described species: *T. jareckiorum* n. sp. from the Antilles and *T. salazarae* n. sp. from the Mexican Pacific coast. The main differences are the type of parapodial papillae and the type or articulation in notochaetae; thus, *T. havaica* n. comb. has markedly capitate parapodial papillae, each with a marked distal expansion, whereas the other species have digitate or slightly capitate papillae. *T. havaica* n. comb. is also unique in having an irregular pattern of articulation, having a longer article between a series of smaller ones. The other species have a gradual change in article size throughout the chaeta.

Trophoniella hospita (Fauchald, 1972) n. comb. (Figs 14A; 16)

Piromis hospitis Fauchald, 1972: 229-231, pl. 48, figs a-e (*non P. hospitis* – Blake 2000: see *Trophoniella harrisae* n. sp.).

TYPE MATERIAL. — **Eastern tropical Pacific**, **Gulf of California.** Holotype (LACM-AHF 1178) and paratypes (LACM-AHF 1214), off SW Punta Arena, Carmen Island, R/V *Velero IV*, stn 1746 (25°48'50"N, 111°15'00"W → 25°49'40"N, 111°15'30"W), 95-115 fathoms, sand, mud, pebbles, 18.III.1949 (paratypes 1 posterior fragment and 9 anterior fragments: 17-33 mm long, 4-5 mm wide, cephalic cage 10-13 mm long, 20-31 chaetigers, dorsal lappets present in chaetigers 2-22; first anchylosed neurohooks in chaetigers 22-28).

ADDITIONAL MATERIAL. — **Eastern tropical Pacific.** Anterior fragment (LACM-AHF 2491), Dewey Channel, opposite San Eugenio Point, R/V *Velero III*, stn 1260 (27°49'50"N, 115°06'05"W → 27°49'35"N, 115°06'00" W), 23-26 fathoms, coralline rock, 27.II.1941 (68 mm long, 4 mm wide, cephalic cage 5 mm long, 68 chaetigers; dorsal lappets in chaetigers 2-25). — Anterior fragment (LACM-AHF 2492), 1 mile off Perico Point, Carmen Island, Gulf of California, R/V *Velero IV*, stn 1758 (25°57'30"N, 111°06'07"W → 25°57'31"N, 111°05'54"W), 15-18 fathoms, coarse sand, 21.III.1949 (52 mm long, 5 mm wide, cephalic cage 11 mm long, 40 chaetigers; dorsal lappets in chaetigers 2-22).

DISTRIBUTION. — Gulf of California, western Mexico, in mixed bottoms at 30-230 m depth.

DESCRIPTION

Holotype (LACM-AHF 1178), anterior fragment, slightly damaged (Fig. 14A). Tunic papillated, with fine sediment particles, especially dorsally. Body club shaped, tapering posteriorly, stiff, 40 mm long, 7 mm wide, cephalic cage 14 mm long, 30 chaetigers. Body papillae long, capitate, arranged in longitudinal rows, two dorsally, four ventrally; dorsal papillae forming triangular, blunt lappets (Fig. 16A, C), directed anteriorly, present to chaetiger 26, largest in chaetigers 2-10, diminishing in size posteriorly; ventral papillae forming large, rounded lobes only in chaetigers 1-5, posterior ones smaller.

Anterior end slightly everted in holotype (Fig. 16B). one paratype dissected to study the anterior end. Prostomium low, eyes large, brownish (posterior eyes not seen). Caruncle well developed, running through the tongue-like branchial plate. Palps very large; palp keels reduced, slightly pigmented. All lips invaginated, probably due to contraction during preservation. Branchiae cirriform, thin, sessile on a tongue-like protuberance, arranged in two lateral groups, filaments arranged in rows, more than 100 filaments per group; most shorter than palps. Nephridial lobes not seen.

Cephalic cage chaetae twice as long as body width. Chaetigers 1-3 involved in the cephalic cage; chaetae arranged in short series, dorsolateral in chaetiger 1, lateral in chaetigers 2-3; 9-10 noto- 7-8 neurochaetae per bundle, carrying peduncled epizoic organisms (hydroids?). Anterior dorsal margin of first chaetiger with a median, pentafid

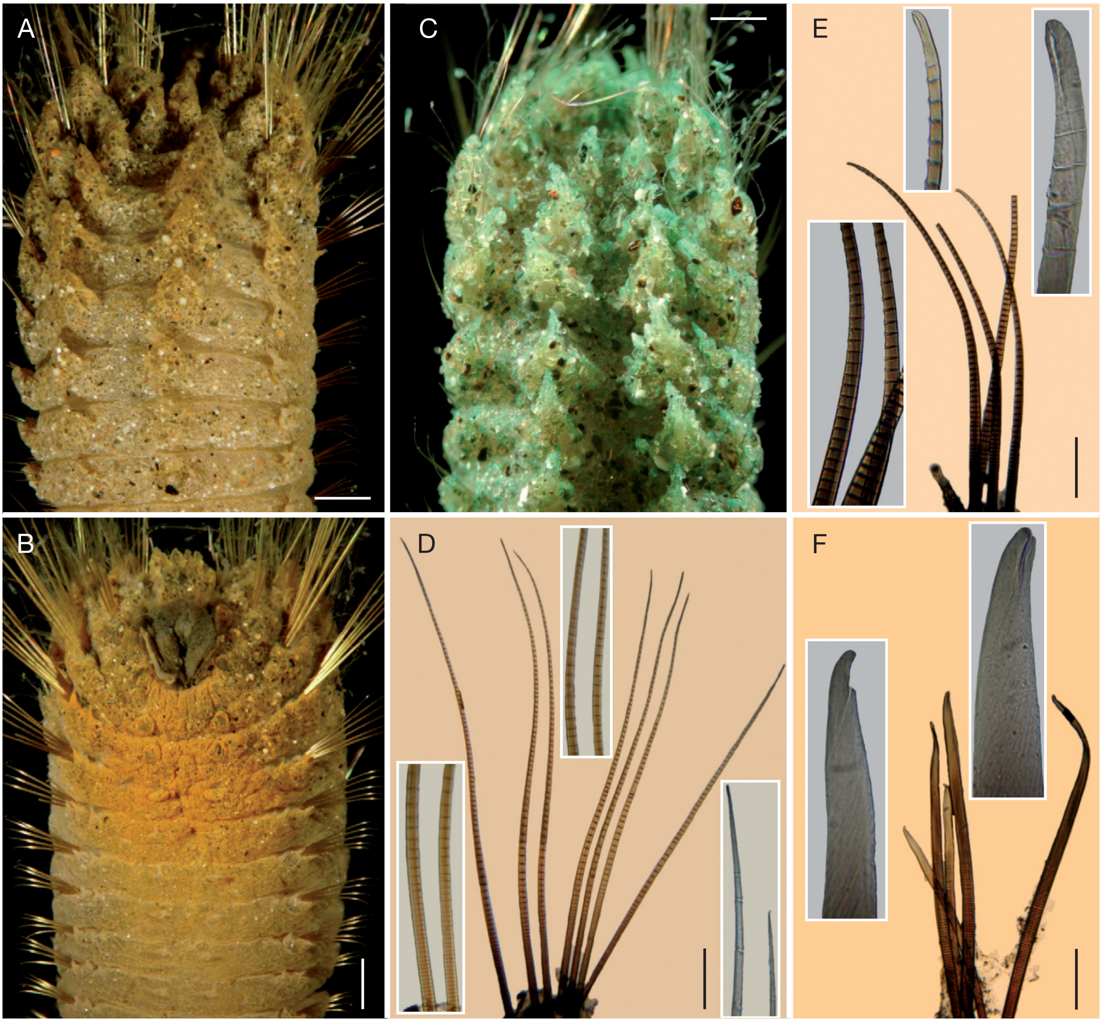

FIG. 16. — *Trophoniella hospita* (Fauchald, 1972) n. comb.: **A**, holotype (LACM-AHF 1178), anterior end, dorsal view; **B**, same, anterior end, ventral view; **C**, non-type specimen (LACM-AHF 2492), anterior end, dorsal view; **D**, same, chaetiger 18, notochaetae (inserts: basal, medial and distal notochaetal regions); **E**, same, chaetiger 20, neurochaetae (inserts: medial and two enlargements of the same chaetal tip); **F**, same, chaetiger 30, neurochaetae (inserts: two chaetal tips). Scale bars: A, B, 1.8 mm; C, 1 mm; D, 375 µm; E, 360 µm; F, 225 µm.

lobe, projected anteriorly, slightly eroded. Anterior chaetigers (1-8) with longer notopodial papillae forming notopodial lobes and dorsal tubercles, directed anteriorly, diminishing in size posteriorly. Chaetigers 1-3 of about the same size. Chaetal transition from cephalic cage to body chaetae gradual; bidentate neurohooks resembling anterior neurochaetae present from chaetiger 5; anchylosed neurohooks present from chaetiger 25. Gonopodial lobes not seen.

Parapodia better developed in anterior chaetigers; median and posterior ones with elongated notopodial papillae, chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia with one prechaetal papilla, one large postchaetal, and 2(-3) inferior smaller papillae.

Median notochaetae arranged in short oblique series (becoming transverse, U-shaped by chaetiger 20), 7-8 per bundle (up to 10 by chaetiger 30 in other specimens), as long as ⅓ body width; all notochaetae multiarticulated capillaries, each with articles short basally, becoming long medially, longer distally (Fig. 16D, inserts). Neurochaetae multiarticulated capillaries in chaetigers 1-4; multiarticulate bidentate hooks from chaetiger 5, each with short, basal articles and long articles medially and distally, arranged in transverse series, 4-5 per neuropodium (Fig. 16E). Anchylosed bidentate neurohooks starting by chaetiger 25 (by chaetiger 28 in other specimens); each with short, anchylosed articles present to the subdistal straight region, blade hyaline (with fine oblique striae), bidentate but accessory tooth often eroded (Fig. 16F). Posterior chaetigers (observed in paratypes) having most neurohooks with eroded tips, looking blunt, but a few retaining the bidentate tip.

Posterior end (observed in a single posterior end in paratype lot) subdistally swollen, sediment particles restricted to the middorsal line (other posterior regions with sediment covering the whole dorsal surface); pygidium with anus dorsoterminal, no anal cirri.

REMARKS

Trophoniella hospita n. comb. resembles *T. harrisae* n. sp. by having dorsal paired lappets along several anterior chaetigers. They differ because these lappets are more foliose and basally narrower in *T. hospita* n. comb., whereas they are thicker and wider basally in *T. harrisae* n. sp., and because they extend through a different number of chaetigers or body length: in *T. hospita* n. comb. they frequently reach up to chaetiger 20, whereas in *T. harrisae* n. sp. they reach up to chaetiger 40. The original description regarded the posterior hooks as entire, but the tips might be eroded, as indicated by Blake (2000), and herein confirmed.

Trophoniella incerta (Augener, 1918) n. comb.
(Fig. 17)

Stylarioides incertus Augener, 1918: 442-444, pl. 6, figs 156, 157, pl. 7, figs 235, 236, textfig. 65.

TYPE MATERIAL. — Lost; originally described from “West Africa”, without further details.

DISTRIBUTION. — Western Africa, probably in shallow water.

DIAGNOSIS. — Body cylindrical, slightly tapering posteriorly (Fig. 17A). Tunic without sediment cover; papillae minute (Fig. 17B). Cephalic cage chaetae slightly longer than body width. Notopodia (Fig. 17C), and neuropodia (Fig. 17D) with two long, capitate papillae. Median notochaetae with articles short basally, long medially, distally medium-sized, 7-9 per bundle (Fig. 17E). Anchylosed neurohooks from chaetiger 6, each with short rings present to the subdistal, straight region; median chaetigers with bidentate neurohooks (Fig. 17F), posterior chaetigers with blunt, unidentate tips (Fig. 17G).

REMARKS

Hartman (1953: 51) thought *Trophoniella incerta* n. comb. could be the same as *Piromis arenosus* because neurohooks are bifid. However, the bifid neurohook that Augener illustrated (his fig. 65b, herein redrawn as Fig. 17F) is anchylosed, with very short rings, not provided with long articles as in *Piromis*. The species has apparently not been collected again and regretfully, there was no clear indication about the type locality.

Trophoniella indica
(Fauvel, 1928) n. comb., n. stat.
(Fig. 18)

Stylarioides eruca indica Fauvel, 1928: 95, 96, fig. 3h-k; 1930: 42, 43, fig. 10h-l; 1932: 180; 1953: 347, fig. 170h-l. — Al-Hakim & Glasy 2004: 38.

TYPE MATERIAL. — **Indian Ocean**, **Bay of Bengal.** 1 slide (IRFA M-33’) with cephalic cage chaetae and neurohooks from anterior chaetigers, in poor shape, from type material, Krusadai Island, Madras, India.

ADDITIONAL MATERIAL. — **Indian Ocean, Andaman Sea.** 1 slide (IRFA R-29) with neurohooks from several chaetigers, including posterior ones, Vancauri, Nancowry Island, Nicobar Islands, India.
Bay of Bengal. 15 specimens (LACM-AHF 2493), International Indian Ocean expedition, northern Indian Ocean, stn RH 30, Madras, 2.5 km SE off harbor, directly E of the University building, 15 m, gray mud with little sand, 18.III.1964, H. Sanders (2.0-15.0 mm long, 11-50 chaetigers; smaller specimens having 16-20 chaetigers, with sediment particles restricted to the anterior and median regions and anchylosed neurochaete from chaetigers 11-13).

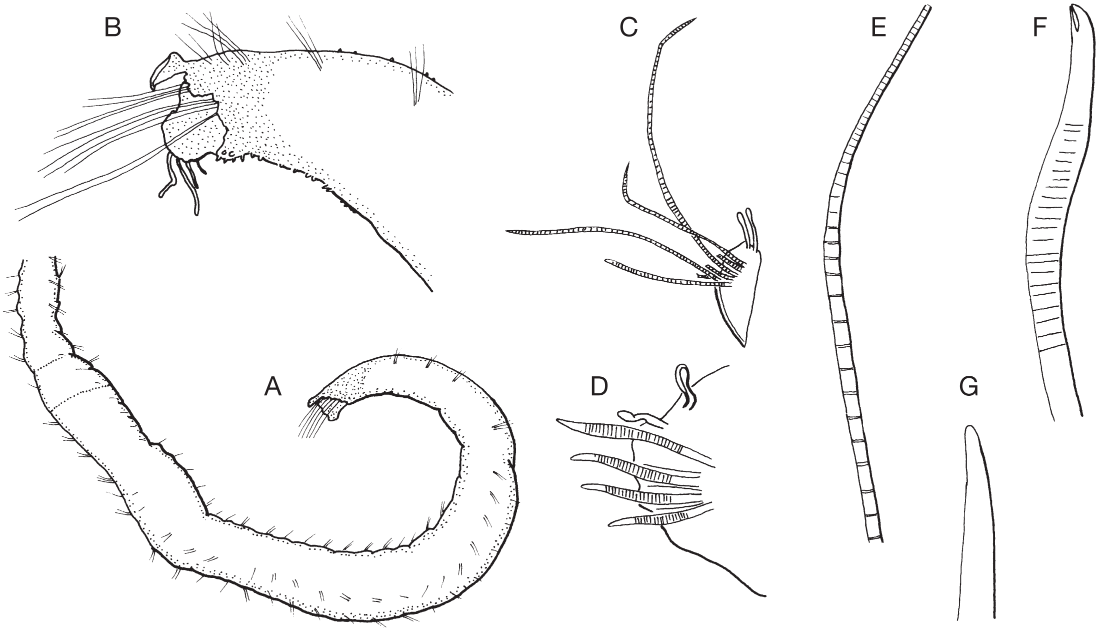

Fig. 17. — *Trophoniella incerta* (Augener, 1918) n. comb., redrawn from Augener 1918: **A**, lateral view; **B**, anterior end, lateral view, most branchiae lost; **C**, median notopodium; **D**, median neuropodium; **E**, notochaeta from median chaetiger; **F**, neurohook from median chaetiger; **G**, neurohook from posterior chaetiger.

Gulf of Carpentaria, Australia. 1 anterior fragment (NTM 18914), damaged, stn T6a (15°21.77'S, 136°30.70'E), Bing Bong, McArthur River, no depth data, 17.III.1993, Marine Ecology Unit (17 mm long, 1.5 mm wide, cephalic cage 3.5 mm long, 32 chaetigers). — 1 complete specimen (NTM 18915), broken in 2 pieces, stn T9a (15°22.58'S, 136°31.72'E), Bing Bong, McArthur River, no depth data, 17.III.1993, Marine Ecology Unit. — 1 anterior fragment (NTM 18916), without sediment in the posterior region, stn T4d (15°22.65'S, 136°30.30'E), Bing Bong, McArthur River, no depth data, 17.III.1993, Marine Ecology Unit (13 mm long, 2 mm wide, cephalic cage 3.5 mm long, 29 chaetigers).

Distribution. — Indian Ocean, from the Krusadai Island, India, to northeastern Australia, in shallow water.

Description

Complete specimen (NTM 18915), broken in two pieces (Fig. 18A), slightly damaged; body with first three chaetigers reddish, posterior end pale, in regeneration (Fig. 18B). Tunic papillated, dorsally and ventrally with large sediment particles (sand, shell fragments, forams and other large particles; NTM 18916 without sediment cover in the posterior region). Body cylindrical, slightly swollen medially, 19.5 (16 + 3.5) mm long, 2 mm wide, cephalic cage 3 mm long (chaetiger 1 chaetae lost), 38 (26 + 12) chaetigers. Body papillae long, capitate, sparse, arranged in longitudinal rows, five dorsally, four ventrally, difficult to detect because of the sediment particles.

Anterior end observed in another specimen (NTM 18916). Cephalic hood tube long, made of two articles, basal ring pigmented, papillated (mostly eroded), distal ring smooth, transparent, margin smooth. Anterior end distorted by eversion of the anterior gut. Prostomium low, no eyes. Caruncle well developed, reaching the end of the branchial tongue-like plate. Palps cylindrical, long, medially and distally eroded; palp keels low, reduced. Lips not detectable due to the anterior gut eversion. Branchiae cirriform, sessile on tongue-like branchial plate, basally narrowed, arranged in two lateral groups, each with about 18 filaments. Branchial filaments longer basally, shorter distally, all shorter than palps.

Nephridial lobes basal, cirriform, elongate, separate from the branchial plate.

Cephalic cage (damaged) chaetae 1.5 times longer than body width. Chaetigers 1-3 involved in the cephalic cage; chaetae of chaetiger 1 arranged in short dorsal and ventral series; others in short ventrolateral series. Chaetiger 1 with two chaetae per bundle, one neurochaeta broken; chaetiger 2 with 2-3 chaetae per bundle; chaetiger 3 with five chaetae per bundle. Anterior dorsal margin of first chaetiger papillated, with a median projection with 1(-2) distal papillae. Anterior chaetigers with conical notopodial lobes anteriorly directed, without especially long papillae (Fig. 18C). Chaetigers 1-3 progressively larger. Chaetal transition from cephalic cage to body chaetae gradual; anchylosed, bidentate neurohooks start by chaetiger 14. Gonopodial lobes not seen.

Parapodia poorly developed; chaetae emerge from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia as short lobes with 4-6 papillae per bundle, being reduced to 2-3 per bundle in posterior chaetigers.

Median notochaetae arranged in short longitudinal series, 5-6 per bundle, as long as ⅓ body width; all notochaetae multiarticulated capillaries, each with articles short basally and medially, distally long (Fig. 18D, inserts). Neurochaetae multiarticulated capillaries in chaetigers 1-3, replaced by similar bidentate hooks from chaetiger 4, each with a distal swelling, tips bidentate (Fig. 18E); replaced completely by chaetiger 14 with smaller, anchylosed hooks. These neurohooks curved distally, darker, neurohooks arranged in transverse series, 4-5 per bundle, each with short rings present to the subdistal, slightly expanded region, blade hyaline, tip bidentate, accessory tooth foliose, passing the fang (Fig. 18F).

Posterior end tapering to a blunt cone (Fig. 18B), pygidium without sediment, probably in regeneration, with anus terminal; no anal cirri.

REMARKS

The type material of *Stylarioides eruca indica*, originally deposited in Calcutta, was not available. This combination was originally published as a variety, which would make it unavailable (ICZN 1999: art. 45.6.3), but it became available because Hartman (1959: 421) listed it as a subspecies (ICZN 1999: art. 45.6.4.1). This species, however, does not belong in *Piromis*, but rather fits *Trophoniella* because its median and posterior neurochaetae are anchylosed, and it differs from other species in the same genus to such a degree that it deserves a new status as *T. indica* n. comb., n. stat.

Fauvel (1928: 7) provided very short description and few illustrations for *S. eruca indica.* He regarded his new variety as closely allied to *Piromis* (*olim Stylarioides*) *eruca* Claparède, 1868 but differing by having longer and thinner neurochaetae. In fact, their neurochaetae are markedly different because in *Trophoniella* they are anchylosed, or provided with very short anchylosed articles or rings, reaching the medial or subdistal chaetal regions, and the hooks can be subdistally expanded, hyaline, whereas in *Piromis* neurohooks have longer articles, which are actually articulated, rarely distally expanded, and articles continue to the subdistal chaetal part.

Trophoniella indica n. comb., n. stat. resembles *T. enigmatica* n. sp. from the Mediterranean Sea and eastern Atlantic because both have dorsal tubercles. They differ, however, besides the branchial features, in the relative start of the anchylosed neurohooks, and about the size of the accessory tooth; thus, in *T. indica* n. comb, n. stat. the anchylosed neurohooks start by chaetiger 14, whereas they start by chaetiger 40 in *T. enigmatica* n. sp., and the distal tooth is longer than the fang in *T. indica* n. comb, n. stat., whereas it is as long as fang in *T. enigmatica* n. sp.

Many juveniles or recently recruited specimens (LACM-AHF), 0.9-15 mm in length, show that the sediment cover pattern is fixed early during ontogeny. Thus, most specimens have sediment particles throughout the body, but the relative sediment particles density is size-dependent. This might imply that particles are fixed depending on the size, abundance and relative exposure of the body papillae and, at the same time, dorsal tubercles might be size-dependent and consequently, trying to identify some juveniles with the key above which is based on adults, might be misleading. On the contrary, the start of anchylosed neurohooks changes throughout the juvenile development

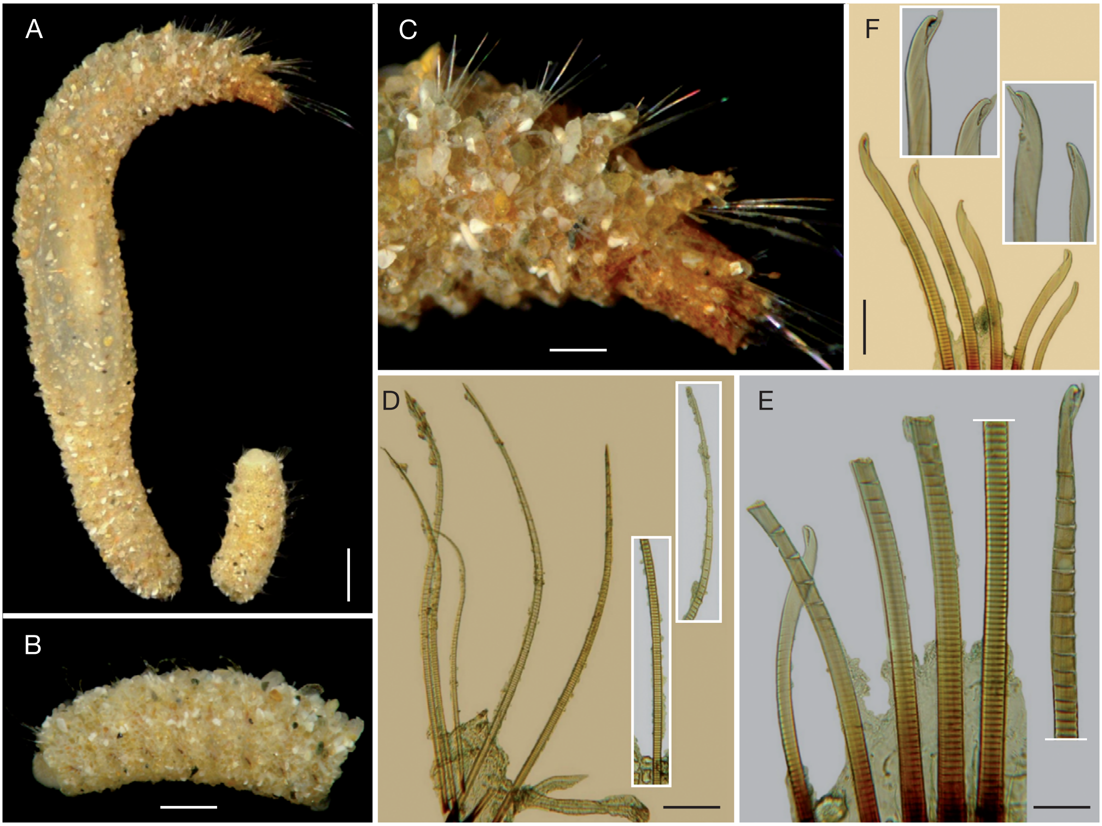

FIG. 18. — *Trophoniella indica* (Fauvel, 1928) n. comb., n. stat., complete specimen (NTM 18915): **A**, lateral view; **B**, posterior region, lateral view; **C**, anterior end, lateral view; **D**, chaetiger 10, notochaetae (inserts: basal and distal notochaetal regions); **E**, chaetiger 18, neurochaetae (longest multiarticulate hook separated in two pieces); **F**, chaetiger 32, neurochaetae (inserts: tips of neurochaetae). Scale bars: A, 1.25 mm; B, 0.6 mm; C, 0.4 mm; D, F, 90 µm; E, 40 µm.

because their start is apparently displaced posteriorly during ontogeny; thus, a 1.7 mm long juvenile has them from chaetiger 5, a 2.3 mm long has them from chaetiger 7, a 2.5 mm long has them from chaetiger 9, and a 15 mm long has them from chaetiger 14, as in the adult.

Trophoniella jareckiorum n. sp.
(Fig. 19)

TYPE MATERIAL. — **Western Atlantic Ocean, Caribbean Sea.** Holotype (LACM-AHF 2494), British Virgin Islands, Guana Island, White Bay, *c.* 15 m off shore, shoreward of first two finger reefs (18°28'27"N, 64°34'34"W), artificial reef matrix structures, 1.5 m, 9.VII.2000, T. Zimmerman, G. Hendler, R. Ware, K. Fitzhugh. — 2 paratypes (LACM-AHF 2495), a complete specimen and an anterior fragment, damaged, body and tunic irregularly broken, British Virgin Islands, Guana Island, N bay lagoon, rocky intertidal, just W of wooden dock (18.482°N, 64.575°W), algal covered coral rubble, snorkel, hand, 25.VII.1999, Don Cadien (complete 20 mm long, 2 mm wide, cephalic cage 3 mm long, 49 chaetigers; gonopodial lobes not seen).

ADDITIONAL MATERIAL. — **Western Atlantic Ocean, Caribbean Sea.** Anterior fragment (LACM-AHF 2496), British Virgin Islands, Guana Island, N bay lagoon, W end, directly offshore from house and wooden dock (18°26'54"N, 64°34'29"W), algae off coral rubble, snorkel, scraper, 0.5 m, 3.VII.2000, K. Fitzhugh (6 mm long, 1.5 mm wide, cehalic cage 1.5 mm long, 27 chaetigers; tunic transparent, branchial plate entire). — 3 specimens (LACM-AHF 2497), juveniles, British Virgin Islands, Guana Island, Long Point, *c.* 70 m SE of small dock, in a protected area at bottom of furrow (18.486°N, 64.583°W), 12-15 ft, SCUBA, hand, 5.VII.2000, T. Zimmerman & G. Hendler (3-12 mm long, 1-2 mm wide, cephalic cage 1-2 mm long, 24-40 chaetigers; smallest juvenile with first neurohooks in chaetiger 4).

TYPE LOCALITY. — Guana Island, British Virgin Islands.

DISTRIBUTION. — British Virgin Islands, in shallow water (1-2 m) mixed bottoms.

ETYMOLOGY. — The specific name is derived after Drs Henry Jarecki and Lianna Jarecki. The former is the head of the family which owns Guana Island, and who recognised the value of a protected nature preserve on this beautiful island, and the latter established the Guana Marine Science Program under which these specimens were collected (see Martin 2002 for other details about the expedition).

DESCRIPTION

Holotype whitish, without posterior region (Fig. 19A). Tunic papillated, rugose, partially eroded into an areolated surface, without sediment particles. Body cylindrical, slightly tapering posteriorly, posterior section slightly swollen by contraction, 14 mm long, 3 mm wide, cephalic cage 4 mm long, 51 chaetigers. Body papillae cirriform, distally expanded, arranged in three irregularly alternating transverse rows (better seen in non-contracted specimens), and in longitudinal rows as two dorsally and four ventrally (Fig. 19D), ventral papillae smaller.

Anterior end exposed (Fig. 19B, C). Cephalic hood short, smooth, margin smooth. Prostomium low, pale. Eyes dark-brown. Caruncle pale, well developed, extended along ⅔ of the branchial plate, median keel and lateral ridges elevated. Palps pale, thick, twice as long as branchial plate, palp keels pale, rounded. Lips well developed, distorted by pharynx eversion. Branchiae pale, cirriform, sessile on a distally cleft, tongue-like protuberance (entire in juveniles, LACM-AHF 2496), arranged in two lateral groups, in 3-4 longitudinal rows per group, with about 60 filaments per group; filaments longer basally, longest about as long as ⅓ palp length. Nephridial lobes not seen.

Cephalic cage chaetae barely longer than body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short, dorso-lateral or lateral series, 5-6 notochaetae and 4-5 neurochaetae per bundle. Anterior dorsal margin of first chaetiger with a small trilobed projection. Anterior chaetigers with papillae markedly longer than those present in following chaetigers. Chaetigers 1-3 slightly progressively longer. Chaetal transition from cephalic cage to body chaetae abrupt; first anchylosed neurohooks present in chaetiger 5. Ventral gonopodial lobes transverse, oblong, eroded in chaetiger 5.

Parapodia poorly developed, chaetae emerge from the body wall (Fig. 19D). Parapodia lateral, median neuropodia ventrolateral. Notopodia with a basal and a lateral papillae, longest papillae about ⅓ as long as notochaeta. Neuropodia with smaller papillae.

Median notochaetae arranged in short, transverse series, 4-5 notochaetae per bundle, about as long as ¼-⅕ body width; all notochaetae multiarticulated, each with small articles in a short basal portion, then medium-sized and longer articles medially and distally (Fig. 19F). Neurochaetae multiarticulated capillaries in chaetigers 1-4, falcate anchylosed neurohooks from chaetiger 5, arranged in transverse series, five per bundle in most chaetigers (Fig. 19G), only four in posterior chaetigers, each subdistally slightly expanded; depressed, short rings only in the basal region, blade pale, flat, wider than handle, with tips slightly incurved, entire.

Posterior end not known.

REMARKS

Trophoniella jareckiorum n. sp. is closely allied to *T. salazarae* n. sp. from the tropical Pacific Mexican coast, because both have an opaque tunic which does not include sediment grains. They differ especially on the general pigmentation pattern and in the number and type of notochaetae; thus, *T. jareckiorum* n. sp. is whitish, whereas *T. salazarae* n. sp. is grayish to reddish, finely speckled with tiny black spots, has fewer notochaetae (4-5 vs 5-8 per bundle), and has long articles medially and distally, whereas the long articles are restricted to the distal portion in *T. salazarae* n. sp.

Trophoniella lindae n. sp.

(Fig. 20)

Siphonostomum cariboum – Ehlers 1887: 158-161, pl. 42, figs 6-9, pl. 43, fig. 1 (*non* Grube & Ørsted *in* Grube 1859).

Flabelligera cariboea – Treadwell 1939: 280, 281, fig. 96 (*non* Grube & Ørsted *in* Grube 1859).

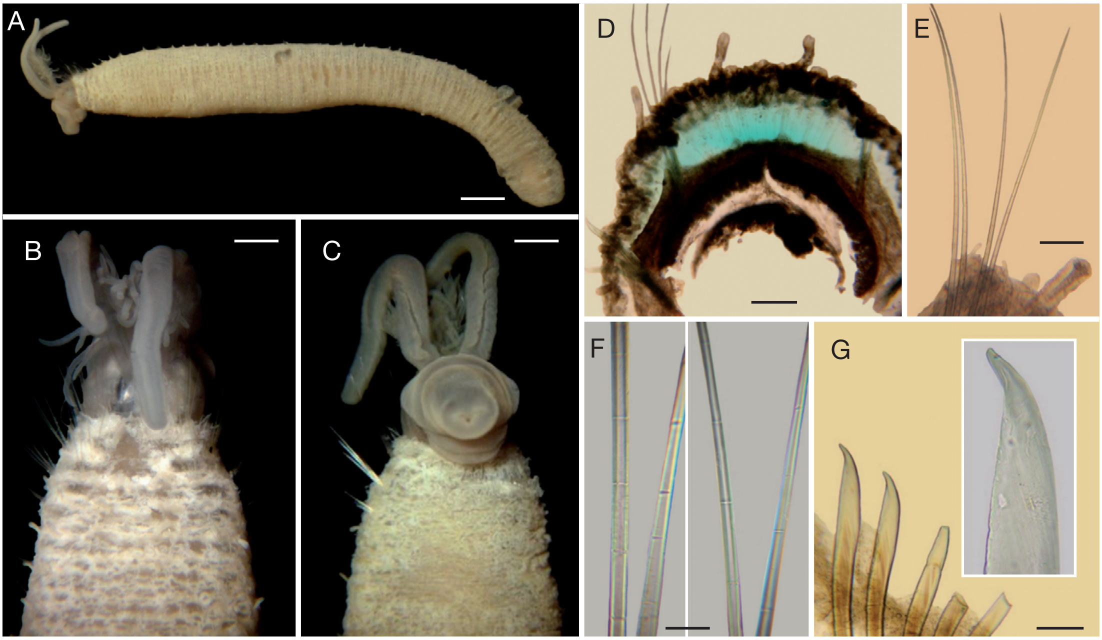

FIG. 19. — *Trophoniella jareckiorum* n. sp.: **A**, holotype (LACM-AHF 2494), lateral view; **B**, same, anterior end, dorsal view; **C**, same, anterior end, ventral view, pharynx exposed; **D**, paratype (LACM-AHF 2495), median fragment, slightly stained with methyl green; **E**, holotype, notopodium from chaetiger 12; **F**, same, notochaetal basal and medial regions; **G**, same, neuropodium from chaetiger 12 (insert: close-up of largest neurohook tip). Scale bars: A, 2.3 mm; B, 0.6 mm; C, 0.7 mm; D, 0.4 mm; E, 110 µm; F, 30 µm; G, 112 µm.

Semiodera cariboum – Hartman 1956: 294, 295 (*non* Grube & Ørsted *in* Grube 1859).

TYPE MATERIAL. — **Southern Caribbean Sea**. Holotype (USNM 1156945) and 3 paratypes (USNM 1156946), 5 km off S of Guayacancito, Isla Margarita, Venezuela, stn M42, in *Thalassia*, 13.II.1977, M. L. Jones (paratypes: 51-112 mm long, 3-8 mm wide, cephalic cage 4-6 mm long, 66-108 chaetigers; first neurohooks from chaetiger 6).

ADDITIONAL MATERIAL. — **Northern Caribbean Sea.** 2 specimens (ECOSUR), 1 complete, regenerating the posterior end, and an anterior fragment, Punta Nizuc, Quintana Roo, Mexico, calcareous rock, 3 m, 31.VIII.1997, L. Carrera & M. A. Ruiz (complete previously dissected, 33 mm long, 4 mm wide, cephalic cage broken, 59 chaetigers).
Southern Caribbean Sea. 1 specimen (UMML), regenerating the posterior end, University of Miami Deep Sea expeditions, R/V *Pillsbury*, stn 428 (09°44'W, 79°22'W), off N Central Panama, 452 m, 20.VII.1966 (15 mm long, 2.5 mm wide, cephalic cage 4 mm long, 49 chaetigers; first neurohooks from chaetiger 6). — 1 specimen (UMML), regenerating the posterior end, University of Miami Deep Sea expeditions, R/V *Pillsbury*, stn 705 (10°45'N, 62°21'W), N Peninsula de Paria, Venezuela, 18 m, 18.VII.1968 (7.5 mm long, 1.5 mm wide, cephalic cage 5 mm long, 30 chaetigers; first neurohooks from chaetiger 6).

TYPE LOCALITY. — Off S of Guayacancito, Isla Margarita, Venezuela, Caribbean Sea.

DISTRIBUTION. — Caribbean Sea, in sea-grasses (*Thalassia*), in shallow water.

ETYMOLOGY. — This species is named after my good friend and colleague Linda Ward, in recognition of her painstaking efforts to compile and update the polychaete bibliography, and especially for her friendship and warm support whenever I visit the USNM.

DESCRIPTION

Holotype complete, cylindrical, slightly tapering posteriorly (Fig. 20A), posterior region slightly damaged, 90 mm long, 7 mm wide, cephalic cage 6 mm long, 97 chaetigers. Tunic papillated, with fine sediment particles dorsally, extending ventrally over chaetigers 5-6 only (Fig. 20B, C); body wall grayish. Larger body papillae in longitudinal rows, dorsal ones barely visible, three per segment, four ventrally; ventral papillae tiny, without sediment.

Anterior end everted in holotype, slightly damaged (Fig. 20B, C), observed in paratypes. Cephalic hood short, margin smooth. Prostomium low, eyes large, black; caruncle well developed, separating the branchial plate in two halves, lateral ridges pale, medial keel darker, basally sinuous. Palps thin, short, palp bases low, rounded (two paratypes with exposed anterior end, slightly everting the anterior gut). Lateral lips thick, dorsal and ventral lips reduced. Branchiae cirriform, most lost, sessile filaments on a tongue-like protuberance, remaining filaments pale basally, dark medially, tips black; arranged in 6-9 longitudinal rows per side, with many filaments each (Fig. 20F). Basal branchiae shorter than palp. Nephridial lobes in external lateral base of branchial plate.

Cephalic cage chaetae as long as $\frac{1}{15}$ body length, or about as long as body width. Chaetigers 1-3 involved in the cephalic cage; first chaetiger displaced dorsally (left notochaetae removed); chaetae arranged in short series, each about the body corners. Chaetiger 1 with about 10 noto- and eight neurochaetae, thereafter about eight chaetae per bundle.

Anterior dorsal margin of first chaetiger papillated, partially damaged (Fig. 20D); chaetigers 1-4 without especially long papillae (some paratypes with epizoic hydrozoans). Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt. Chaetiger 5 with transitional short neurohooks; anchylosed falcate neurohooks from chaetiger 6. Gonopodial lobes not seen in holotype; some paratypes with a ventral transverse slit in chaetiger 5 (once the tunic is removed, a globular pale lobe underneath it; Fig. 20E).

Parapodia better developed in chaetigers 1-4, posterior ones less developed, placed over the body corners. Median neuropodia ventrolateral. Notopodia short conical lobes with one short and a long postchaetal papillae, becoming longer in posterior chaetigers. Neuropodia flat, transverse lobe with two long papillae, one superior, another postchaetal. Noto- and neuropodia distant to each other.

Median notochaetae arranged in short transverse series, 5-6 per bundle, as long as $\frac{1}{5}$-$\frac{1}{6}$ body width; all notochaetae multiarticulated capillaries, each with articles short basally, medium-sized medially, longer distally (Fig. 20G). Neurochaetae long, multiarticulated capillaries in chaetigers 1-4, chaetiger 4 with transition hooks (Fig. 20H), anchylosed neurohooks from chaetiger 5, arranged in J-patterns or oblique series, five hooks anteriorly, 6-7 medially, 4-5 posteriorly; each hook with short rings present to the median region, subdistally slightly expanded, with a discontinuous, oblique, dark spot, tip entire.

Posterior end conical, without long papillae (Fig. 20I); pygidium with anus terminal, no anal cirri (one paratype regenerating its posterior end, anus with several radiating muscular lobes).

Variation

Complete paratypes had bodies fusiform or anteriorly swollen, without posterior end, or regenerating it (51-112 mm long, 3-8 mm wide, cephalic cage 4-6 mm long, 66-108 chaetigers). The relationship of cephalic cage chaetae length to body width (chaetiger 10) was mostly less than 1, with three specimens having a rate ≥ 1. Anchylosed neurohooks start in chaetigers 5-6. Gonopodial lobes were noticed by a short, ventral transverse slit, but once the tunic is removed, they can be seen as pale, rounded lobes. The number of notochaetae can be up to eight per bundle.

REMARKS

Trophoniella lindae n. sp. is closely allied to *T. americana* n. comb. from Galápagos and to *T. tumbensis* n. comb. from Chile because their tunics have sediment particles over the dorsal surface and might expand laterally. However, *T. lindae* n. sp. differs because it has small sediment particles, whereas the two other species have larger particles on their tunics.

There has been much confusion regarding the recognition of this species because Ehlers (1887) described some specimens that he regarded as *Siphonostomum cariboum* Grube & Ørsted *in* Grube, 1859. However, Ehlers' specimens do not belong in *Semiodera* because they do not have a dorsal shield, neither a very thin tunic, nor tiny papillae arranged in transverse rows. Consequently, it has been regarded appropriate to introduce a new name for this common, soft-bottom species, and to separate it from

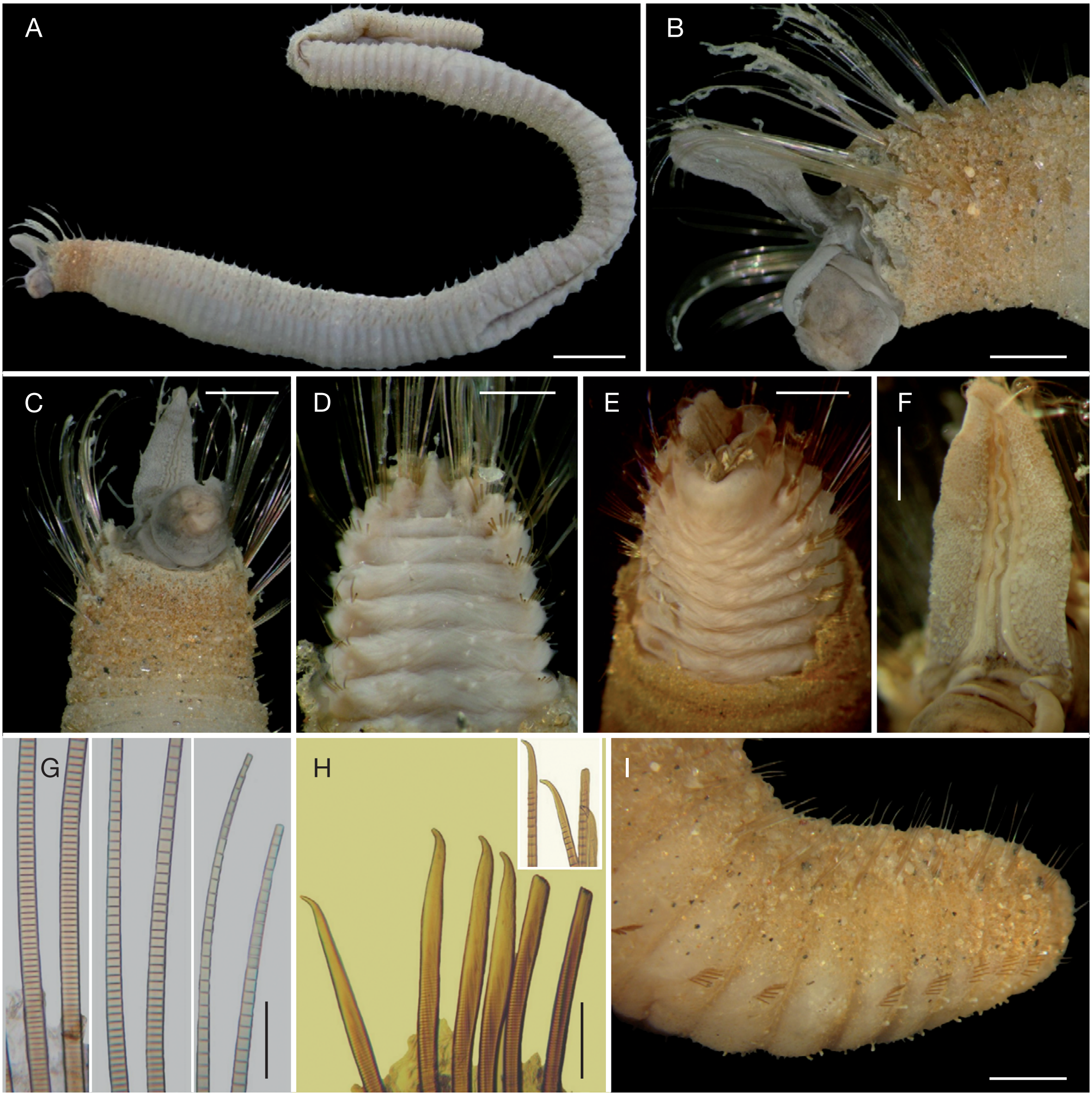

FIG. 20. — *Trophoniella lindae* n. sp.: **A**, holotype (USNM 1156945), lateral view; **B**, same, anterior end, lateral view; **C**, same, anterior end, ventral view; **D**, paratype, without tunic, anterior end, dorsal view; **E**, same, anterior end, ventral view; **F**, another paratype, branchial plate, branchial filaments removed; **G**, another paratype, chaetiger 10, notochaetal basal, medial and distal regions; **H**, same, chaetiger 6, neurohooks (insert: neurochaetal tips, chaetiger 4); **I**, same, posterior end, lateral view. Scale bars: A, 7 mm; B, 1.7 mm; C, 2 mm; D, 1.3 mm; E, 1.4 mm; F, I, 0.9 mm; G, 90 µm; H, 150 µm.

S. cariboum, which besides the above features, is a borer in calcareous substrates. *Semiodera* is revised elsewhere; it could be added that neurochaetae are also very different because they are shorter and fewer in this genus, whereas those present in *Trophoniella* are larger and more abundant.

Trophoniella minuta
(Blanchard *in* Gay, 1849) n. comb.
(Fig. 21)

Siphostoma minutum Blanchard *in* Gay, 1849: 36. — Rozbaczylo 1985: 161.

Pherusa minuta – Quatrefages 1866: 480.

Pherusa heteropapillata Hartmann-Schröder, 1965: 227, figs 222, 223. — Rozbaczylo 1985: 160.

TYPE MATERIAL. — **Southeastern Pacific Ocean**. Holotype of *S. minutum* (MNHN 628), Chile (specific locality not stated, probably Valparaiso), 1834, Fontaine (complete, some parapodia removed, body wall with a transverse anterior fracture; 14 mm long, 3 mm wide, cephalic cage 4 mm long, 59 chaetigers; first anchylosed neurohooks in chaetiger 6). — Paratypes of *P. heteropapillata* (ZMH unnumb.), off Puerto Estero Cisne, Isla James, Los Chones Archipelago, Chile, mussel-bed, shallow water, 11.VII.1958, Stuardo (4 complete 40-43 mm long, 5.0-10.5 mm wide, cephalic cage 10.0-10.5 mm long, 82-84 chaetigers; all with anchylosed neurohooks from chaetiger 6; description based on the best paratype).

ADDITIONAL MATERIAL. — **Southeastern Pacific Ocean**. 1 specimen (MCZ 55674), Paraca Bay, Peru, no further data (108 mm long, 11 mm wide, cephalic cage 10.5 mm long, 87 chaetigers). — 1 specimen (MCZ 55675), Valparaiso, Chile, no further data (70 mm long, 10 mm wide, cephalic cage 9 mm long, 78 chaetigers). — 1 specimen (LACM-AHF 2498), most chaetae undamaged, R/V *Velero III*, stn 376 (14°15'35"S, 76°11'35"W), E of Viejas (or Independencia) Island, Independencia Bay, Peru, 7 fathoms, rock, 13.I.1935 (15 mm long, 4 mm wide, cephalic cage 6 mm long, 60 chaetigers; gonopodial lobes visible once the tunic is removed, low rounded lobes on the anteroventral surface of chaetiger 5).

DISTRIBUTION. — From Peru to Chile, in shallow water along rocky or mixed bottoms.

DESCRIPTION

Holotype (MNHN 628) pale, soft, preserved in alcohol (Fig. 21A). Paratypes of *Pherusa heteropapillata* (ZMH unnumb.) large, dark, stiff (Fig. 21D). Body fusiform, wider anteriorly, tapering posteriorly, 43 mm long, 9 mm wide, cephalic cage 10 mm long, 84 chaetigers. Tunic sparsely papillated, without sediment particles (Fig. 21B, C), surface wooly with fine to very fine sediment particles (Fig. 21E). Body papillae thin, globose, most not exposed, few larger papillae arranged in longitudinal rows, two dorsal, four ventral, distally exposed (more clearly seen in holotype).

Cephalic hood not exposed; anterior end observed by dissection of one paratype; cephalic hood short, dark, margin apparently smooth. Prostomium blackish, low; eyes large, black. Caruncle well developed, reaching the margin of branchial lobe; median keel rounded, grayish, tapering posteriorly, becoming flat by the middle of branchial lobe; marginal ridges flat, darker than median keel. Palps reduced, very short, the left one longest, about ¼ as long as branchial lobe, smooth; palp keels reduced, low, rounded. Lips fused in an oral tube (details incomplete because it was damaged by dissection). Branchiae cirriform, maculated, on a tongue-like protuberance, separated in two lateral groups, arranged in rows; each group with about 200 filaments, basal branchiae longest, decreasing in size towards the margin. Nephridial lobes short, filiform, basally darker, placed in the inner basal margin of branchial groups, not clearly separated from them.

Cephalic cage chaetae about ¼ as long as body length, or as long as body width. Chaetigers 1-3 involved in the cephalic cage; chaetae arranged in short dorsolateral series in chaetigers 1-2, lateral in chaetiger 3; chaetiger 1 with 12 noto- and six neurochaetae; chaetiger 2 with six chaetae per bundle, chaetiger 3 with 6-7 chaetae per bundle. Anterior dorsal margin of first chaetiger much contracted, not visible dorsally or ventrally. Anterior chaetigers without long papillae. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt; falcate, anchylosed neurohooks present from chaetiger 6. Gonopodial lobes not seen (MCZ 55674 with black tiny papillae in chaetiger 5; only seen after removing the tunic).

Parapodia poorly developed, chaetae emerging from the body wall (Fig. 21E). Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia low, with two larger papillae per bundle, one suprachaetal, the other infrachaetal. Noto- and neuropodia distant to each other.

Median notochaetae arranged in transverse series; 11-12 per bundle, as long as ¼ body width; all notochaetae multiarticulated capillaries, each with articles short along the chaeta (Fig. 21F). Neurochaetae multiarticulated capillaries in chaetigers 1-5, becoming shorter in chaetigers 4-5; falcate anchylosed neurohooks from chaetiger 6, dark brown, arranged in J-patterns, 5-6 per bundle, each with short rings present to the median region, subdistally tapering, with oblique striae, surface rough, tip entire (Fig. 21G).

Posterior end blunt, pygidium with anus terminal, without anal cirri.

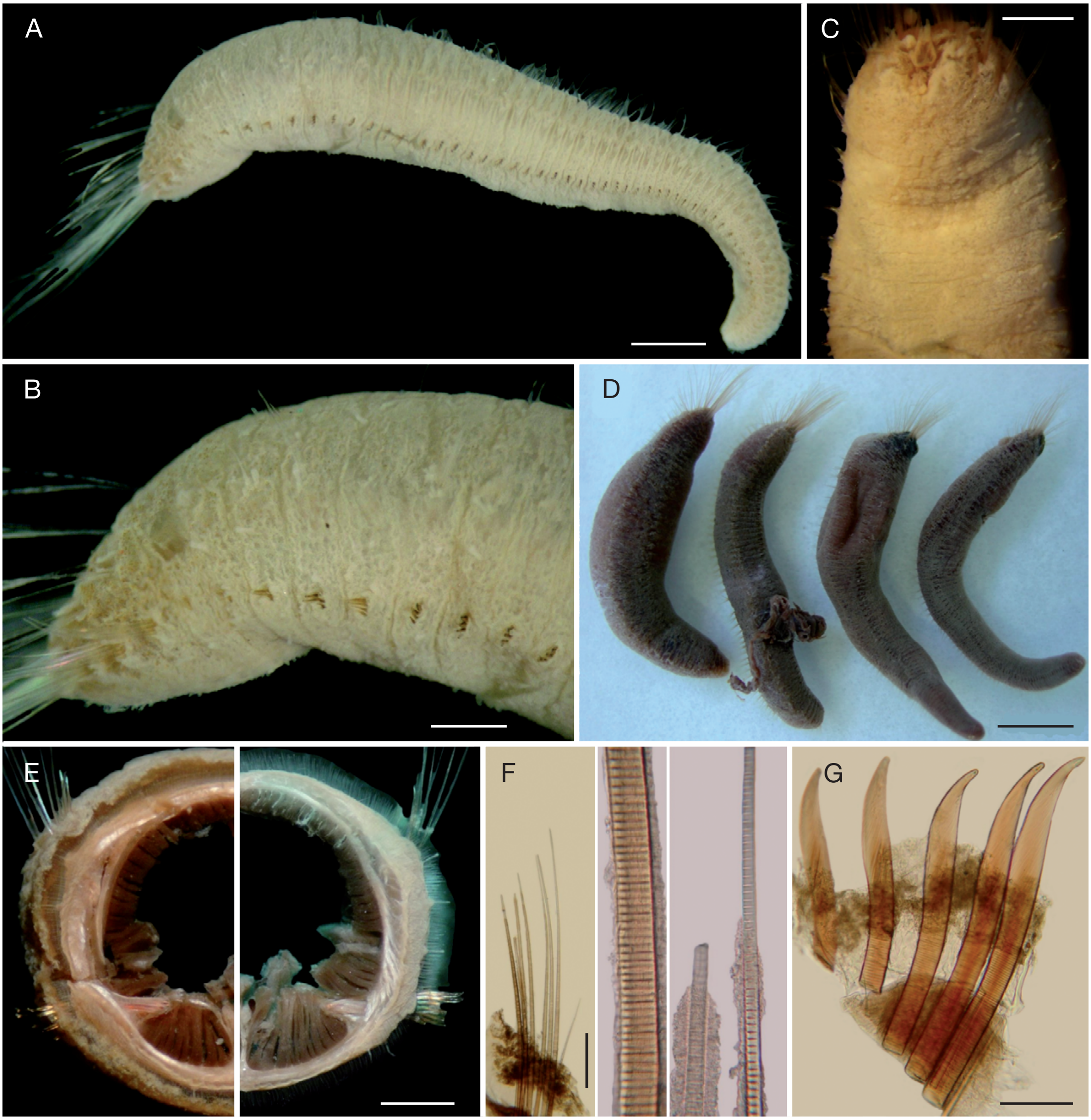

FIG. 21. — *Trophoniella minuta* (Blanchard *in* Gay, 1849) n. comb.: **A**, holotype (MNHN 628), lateral view; **B**, same, anterior end, lateral view; **C**, same, anterior end, ventral view; **D**, paratypes of *Pherusa heteropapillata* Hartmann-Schröder, 1965 (ZMH unnumb.), lateral view; **E**, same, cross sections of median chaetigers with and without tunic (greenish hue is due to methyl green staining); **F**, same, notopodium of chaetiger 13 and notochaetal median and distal regions; **G**, same, neuropodium of chaetiger 20. Scale bars: A, 1.7 mm; B, F, 0.7 mm; C, 0.8 mm; D, 10 mm; E, 1.4 mm; G, 180 µm.

REMARKS

Trophoniella minuta n. comb. resembles other species lacking sediment on the tunic and having digitate or slighlty capitate body papillae, like *T. jareckiorum* n. sp. from the Caribbean Sea and *T. salazarae* n. sp. from the Mexican Pacific coast. However, *T. minuta* n. comb. differs because it has about 10 notochaetae per bundle and has an often smooth and transparent tunic, at least along the anterior region, whereas the two other species have fewer notochaetae and their tunics are papillated and opaque, either whitish as in *T. jareckiorum* n. sp., or grayish to reddish as in *T. salazarae* n. sp.

The reduction of palp size is noteworthy; they could be in regeneration, but it is very rare that both palps had been lost almost at the same time, because they have slightly different size. See *T. grandis* n. comb. for other remarks on the use of the names originally applied by Blanchard and later modified by Quatrefages.

Trophoniella orensanzi n. sp.
(Fig. 22)

Pironis [*sic*] *arenosus* – Rullier & Amoureux 1979: 183 (*non* Kinberg 1867).

TYPE MATERIAL. — **Southwestern Atlantic Ocean, Uruguay**. Holotype (MUNHINA 1116), R/V *Hero* cruise, stn 3A (34°20'S, 53°47'W), off Valizas, N-NW Cabo Polonio, sands, 9 m, 21.VII.1972, J. M. Orensanz.

ADDITIONAL MATERIAL. — **Southwestern Atlantic Ocean, Brazil.** 2 specimens (MNHN 884), anterior fragments, off Rio Grande, R/V *Calypso*, stn 154 (32°15'S, 51°58'W), 18 m, 20.XII.1961.

TYPE LOCALITY. — Off Valizas, Uruguay, in 9 m depth sediments.

DISTRIBUTION. — From Rio Grande, Brazil to Cabo Polonio, Uruguay, in shallow-water sands, in 9-18 m depth.

ETYMOLOGY. — This species is named after my friend and colleague, Dr José M. (Lobo) Orensanz, in recognition of his interesting publications on polychaetes, as a means to thank him for his confidence and support, and because he collected the holotype.

DESCRIPTION

Holotype (MUNHINA 1116) incomplete, anterior fragment, wider anteriorly, tapering posteriorly, medially compressed, slightly damaged (Fig. 22A), 33 mm long, 4 mm wide, cephalic cage 9 mm long, 36 chaetigers. Tunic completely covered with fine sediment particles. Body papillae mostly eroded; parapodial papillae long, capitate; dorsal papillae forming large, blunt, anteriorly directed, dorsal triangular tubercles, present in chaetigers 3-10 (Fig. 22B, C), decreasing in size posteriorly; ventral papillae arranged in two groups per segment, each with 3-5 papillae, probably forming sediment lobes (Fig. 22D), too eroded to confirm their distribution.

Anterior end not exposed, not dissected to avoid further damage; specific details unknown.

Cephalic cage chaetae twice as long as body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short series, dorsolateral in chaetiger 1, lateral in chaetiger 2; chaetiger 1 with 12 noto- and 10 neurochaetae per side; chaetiger 2 with 10 noto- and 14 neurochaetae per side, without epizoans. Anterior dorsal margin of first chaetiger with a median, single, acute lobe, projected anteriorly, with 2-3 marginal papillae. Anterior chaetigers (1-4) with long notopodial papillae forming notopodial lobes, directed anteriorly, diminishing in size posteriorly. Chaetigers 1-3 becoming progressively longer. Chaetal transition from cephalic cage to body chaetae gradual; bidentate multiarticulate neurohooks from chaetiger 6; anchylosed neurohooks present from chaetiger 36. Gonopodial lobes small, rounded, near to neurochaetae in chaetiger 5 (right side, left one damaged).

Parapodia better developed in anterior chaetigers; median and posterior ones with short notopodial lobes, chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia with one prechaetal papilla; other papillae inconspicuous.

Median notochaetae arranged in short longitudinal series, becoming oblique by chaetiger 15; 10-12 per bundle (Fig. 22E), as long as ⅓ body width; all notochaetae multiarticulated capillaries, each with articles short basally, becoming medium-sized medially, long distally (Fig. 22F). Anterior and median neurochaetae multiarticulated, 7-8 per bundle, bidentate capillaries in chaetigers 1-15, most with tips broken; chaetigers 16-35 with similar chaetae but with 1-2 longer, median articles (Fig. 22G); anchylosed, bidentate falcigers from chaetiger 36, arranged in oblique series, 5-6 per bundle, with short rings present almost to the tip, subdistally tapering, most with tips broken, one bidentate, eroded (Fig. 22H).

Posterior end unknown.

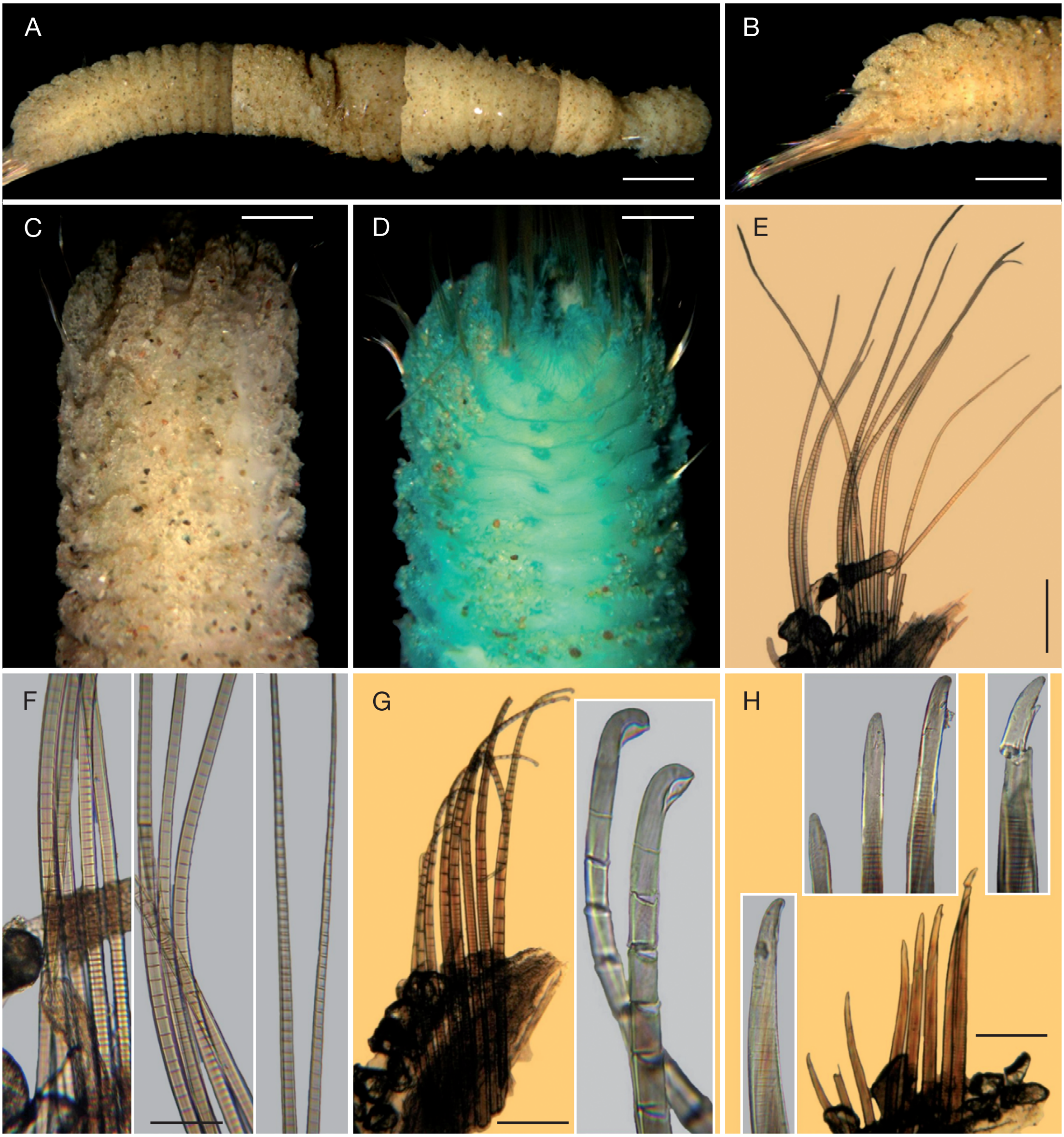

FIG. 22. — *Trophoniella orensanzi* n. sp., holotype (MUNHINA 1116): **A**, dorsal view; **B**, anterior end, lateral view; **C**, anterior end, dorsal view; **D**, anterior end, ventral view with sediment grains eroded; **E**, chaetiger 17, notopodium; **F**, notochaetal basal, medial and distal regions; **G**, chaetiger 26, neurochaetae (insert: chaetal tips); **H**, chaetiger 36, neurochaetae (inserts: chaetal tips). Scale bars: A, 3.3 mm; B, 2 mm; C, 1 mm; D, 0.9 mm; E, 250 µm; F, 75 µm; G, 260 µm; H, 225 µm.

REMARKS

Trophoniella orensanzi n. sp. belongs to the group of species provided with fine sediment particles covering the body and having both notopodial and dorsal tubercles. Besides *T. orensanzi* n. sp., the group includes *T. harrisae* n. sp. and *T. hospita* n. comb.; they differ by the relative extension of the dorsal tubercles along the body; they are less extended in *T. orensanzi* n. sp. being present up to chaetiger 10, whereas they can reach chaetiger 25 in *T. hospita* n. comb., or chaetiger 40 in *T. harrisae* n. sp. Further, this is the only species from the group being recorded from the Atlantic Ocean, whereas the two others are found in the eastern Pacific Ocean.

Trophoniella reishi n. sp.
(Fig. 23)

TYPE MATERIAL. — **Eastern tropical Pacific**, **Gulf of California.** Holotype (ECOSUR-114) and 14 paratypes (3 in BMNH, 5 in ECOSUR, 3 in LACM-AHF, 3 in MNHN), Playa Las Moradas (28°56'25"N, 113°33'20"W), Bahía de Los Angeles, Baja California, Mexico, mixed bottoms, sand and rocks, low intertidal, 25.V.1986, S. I. Salazar-Vallejo (paratypes: 5-30 mm long, 1.5-4.0 mm wide, cephalic cage 3-8 mm long, 32-65 chaetigers; first neurohooks in chaetiger 5-6; some with remains of a thin, pale crust).

ADDITIONAL MATERIAL. — **Eastern tropical Pacific.** 1 specimen (UANL), Isla Coronado (26°70'N, 111°17'00"W), off Loreto, Baja California Sur, Mexico, intertidal, 15.X.1998, J. A. de León-González (12 mm long, 2.5 mm wide, cephalic cage 5 mm long, 53 chaetigers).

TYPE LOCALITY. — Bahía de Los Angeles, Baja California, Gulf of California, Mexico, in the intertidal zone of a mixed (rock and sand) beach.

DISTRIBUTION. — Northwestern coast of the Gulf of California, only known from the type locality, in intertidal areas in mixed shores.

ETYMOLOGY. — The specific name is derived after Dr Donald J. Reish in recognition of his many publications on polychaetes, some dealing with taxonomy but most devoted to ecology and pollution ecology, and especially in recognition of his publication on the ecology of the polychaetes from Bahía de Los Angeles, Gulf of California (Reish 1968), where the type material was collected.

DESCRIPTION

Holotype (ECOSUR-114) complete, barely fusiform, tapering posteriorly (Fig. 23A), pale-brown, 33 mm long, 3 mm wide, cephalic cage 8.5 mm long, 62 chaetigers. Tunic almost without sediment particles, with a thin, partially eroded ochre crust (Fig. 23B, D), smaller paratypes without crust (Fig. 23E). Body papillae abundant, most thin, small, fragile, digitate, many eroded; larger papillae clavate, arranged in longitudinal rows (two dorsal, one lateral and four ventral).

Anterior end observed in one paratype (ECOSUR). Cephalic hood short, margin smooth. Prostomium low, eyes small, black; caruncle well developed, separating the branchial plate in two halves, lateral ridges pale, medial keel darker, basally straight. Palps thick, large, ventrally corrugated, palp bases low, rounded. Lips distorted by the eversion of the pharynx tube. Branchiae cirriform, pale, sessile on a tongue-like protuberance; arranged in two lateral groups, each with filaments in 6-7 longitudinal rows per side, over 100 filaments per group. Basal branchiae as long as palps. Nephridial lobes not seen.

Cephalic cage chaetae as long as ¼ body length, or 3 times longer than body width. Chaetigers 1-3 involved in the cephalic cage, chaetae arranged in short dorsolateral series; chaetiger 1 with 11-12 noto- and six neurochaetae per bundle, chaetiger 2 with eight noto- and six neurochaetae per side, chaetiger 3 with six chaetae per bundle. Anterior dorsal margin of first chaetiger with a median lobe, projected anteriorly (Fig. 23C), with three large distal papillae. Anterior chaetigers with long papillae. Chaetigers 1-3 progressively longer. Chaetal transition from cephalic cage to body chaetae abrupt, falcate anchylosed neurohooks start in chaetiger 5. Gonopodial lobes not seen.

Parapodia lateral, poorly developed; chaetae emerging from the body wall. Median neuropodia ventrolateral. Noto- and neuropodia not forming long lobes; anterior parapodia with abundant, long papillae. Median notopodia with 1-2 infrachaetal, smaller papillae, and one notochaetal, larger papilla (Fig. 23F). Neuropodia with one infrachaetal and 1-2 suprachaetal papillae.

Median notochaetae arranged in short transverse series, 7-8 notochaetae per bundle, about as long as ½-⅓ body width; all notochaetae multiarticulated capillaries, each with articles short basally, medium-sized medially, slighlty longer distally (Fig. 23G). Neurochaetae multiarticulated capillaries in chaetigers 1-4, all articles short, in chaetiger 4 with falcate tip. Falcate, anchylosed, darker neurohooks from chaetiger 5, neurohooks in chaetigers 5-6 almost straight; shorter, falcate neurohooks from chaetiger 7 (Fig. 23H); all neurohooks arranged in

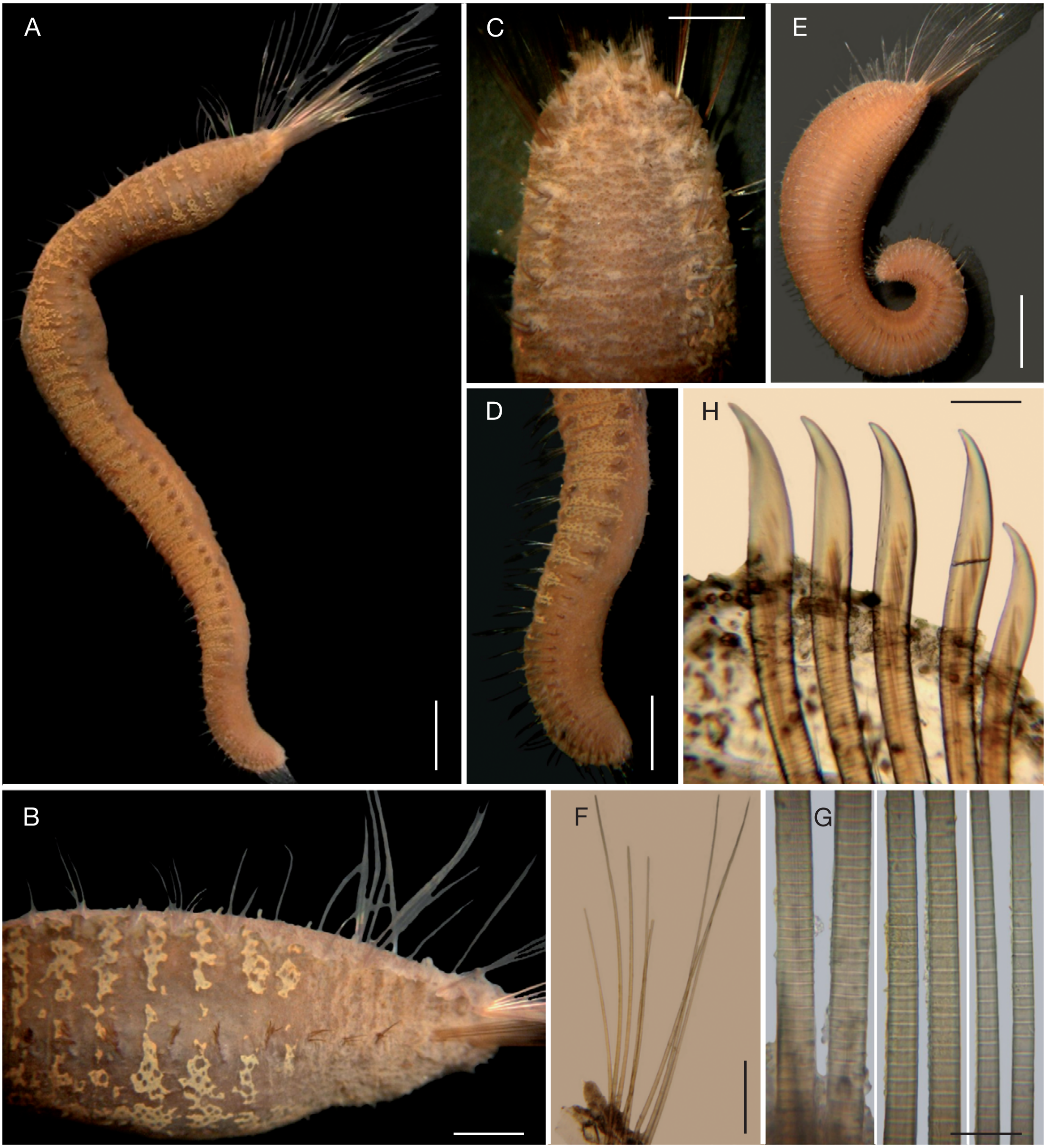

FIG. 23. — *Trophoniella reishi* n. sp.: **A**, holotype (ECOSUR-114), lateral view; **B**, same, anterior end, lateral view; **C**, same, anterior end, dorsal view; **D**, same, posterior end, lateral view; **E**, paratype (ECOSUR), lateral view; **F**, same, chaetiger 10, notopodium; **G**, same, notochaetal basal, medial and distal regions; **H**, same, chaetiger 20, neurochaetae. Scale bars: A, 2.5 mm; B, 0.86 mm; C, 0.9 mm; D, 1.4 mm; E, 3.5 mm; F, 0.3 mm; G, 30 µm; H, 78 µm.

transverse series, or as inverted J-patterns, 4-5 in anterior and posterior chaetigers, 5-6 in median chaetigers, each with short, well-marked anchylosed articles or rings in the embedded part, and less defined in the exposed part, blade pale, tapering, tip falcate, entire.

Posterior end tapering to a blunt rounded tip; pygidium with anus terminal, almost without papillae; no anal cirri.

REMARKS

Trophoniella reishi n. sp. is closely allied to *T. rudis* n. comb. because they have anchylosed, unidentate neurohooks from early chaetigers, and because their tunic barely has sediment particles, being apparently naked. They differ by the relative basic body wall pigmentation and the cephalic cage length. Thus, in *T. reishi* n. sp., the body is dark pink, with fine red spots or rarely pale, and the cephalic cage is twice as long as body width, whereas in *T. rudis* n. comb. the body is solid brown, and the cephalic cage chaetae are 1.0-1.5 times longer than body width.

Trophoniella rigida (Caullery, 1944) n. comb. (Fig. 24)

Brada rigida Caullery, 1944: 39, fig. 30. — Bleeker & Van der Spoel 1992: 126.

TYPE MATERIAL. — **Eastern Indian Ocean**. 3 syntypes (ZMA 1523), Indonesia, Irian Jaya, R/V *Siboga* expedition, stn 163, Strait Selee (= Galewo), W entrance, near Seget anchorage, 29 m, dredge, reef exploration, sand and stones, 18-20.VIII.1899.

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Syntypes variously damaged; most chaetae broken, papillae eroded (Fig. 24A). Body cylindrical, tapering anteriorly, posteriorly rounded, 16-32 mm long, 1.0-2.5 mm wide, cephalic cage 0.5-1.5 mm long, 22-37 chaetigers. Tunic with abundant sand particles dorsally and ventrally, most blackish, more densely in smallest syntype, less densely in largest one. Body papillae scarcely visible, arranged in longitudinal series, four dorsally, two ventrally.

Cephalic hood exposed in one syntype, short, margin crenulated; other features observed by dissection. Prostomium low; eyes not seen. Caruncle thin, depressed, reaching the branchial plate margin. Palps pale, thick, half as long as branchiae; palp keels reduced. Lateral lips fused to dorsal lip, middorsally split; ventral lip well developed, projected anteriorly. Lips projected forming an oral tube. Branchiae cirriform, sessile on a tongue-like protuberance, separated in two lateral groups, each with branchiae arranged in oblique rows, 20-22 filaments per group, most twice as long as palps (Fig. 24E). Nephridial lobes not seen.

Cephalic cage present; most chaetae broken, remaining ones short, shorter than body width (Fig. 24B, C). Apparently only chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short ventrolateral series, with about 4-6 chaetae per bundle. Anterior dorsal margin of first chaetiger smooth. Chaetigers 1-3 becoming slightly longer posteriorly. Chaetal transition from cephalic cage to body chaetae abrupt; anchylosed neurohooks from chaetiger 5 (in smallest syntype). Gonopodial lobes not visible.

Parapodia poorly developed; chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia long lobes, each with one suprachaetal, one infrachaetal and another papilla inferior to the latter, so each chaetal bundle with a superior papilla and two inferior ones in a row, directed ventrally.

Median notochaetae arranged in short longitudinal series, 5-7 per bundle, about as long as ⅕ body width; all notochaetae multiarticulated capillaries, dark yellow, articles short basally, medium-sized in a short medial region, subsequently long to the chaetal tips. Neurochaetae multiarticulated capillaries in chaetigers 1-4; anchylosed neurohooks from chaetiger 5, arranged in transverse series, 4-5 per bundle. Each neurohook dark yellow, with short articles basally and medially, distally yellow, not ringed, tips bifid (Fig. 24G), often eroded.

Posterior end truncated, rounded (Fig. 24D); pygidium retracted; anus terminal, no anal cirri.

REMARKS

Trophoniella rigida n. comb. was originally described in *Brada* Stimpson, 1854, but its branchial plate and anchylosed neurochaetae rather fit what is found in species belonging to *Trophoniella*, hence the new combination.

Trophoniella rigida n. comb. resembles *T. grandis* n. comb. as both have sediment particles covering dorsal and ventral surfaces; they differ by the relative size of sediment grains, development of dorsal

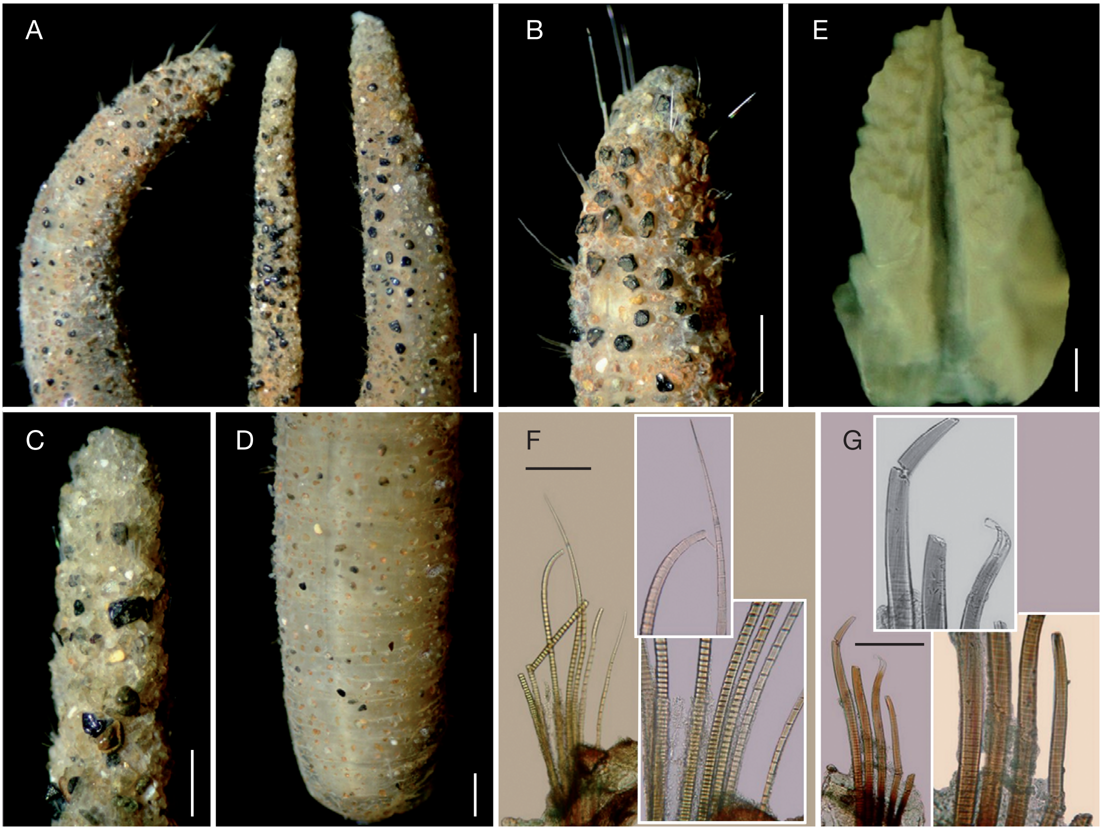

FIG. 24. — *Trophoniella rigida* (Caullery, 1944) n. comb., syntypes (ZMA 1523): **A**, anterior ends of syntypes, lateral or dorsal views; **B**, larger syntype, anterior end, dorsal view; **C**, smaller syntype, anterior end, dorsal view; **D**, larger syntype, posterior end, dorsal view; **E**, branchial plate from medium-sized syntype, frontal view; **F**, medium-sized syntype, notopodium from chaetiger 11 (inserts: basal, median and distal regions); **G**, same syntype, neuropodium from chaetiger 21 (inserts: basal, median and distal regions). Scale bars: A, 1.5 mm; B, 1 mm; C, D, 0.5 mm; E, 0.3 mm; F, 200 μm; G, 115 μm.

tubercles and start of neurohooks. Thus, in *T. rigida* n. comb., sediment grains are large, its anterior chaetigers have no dorsal tubercles, and neurohooks start from chaetiger 5, whereas in *T. grandis* n. comb. sediment grains are small, its anterior chaetigers have dorsal tubercles, and neurohooks start in chaetiger 7.

Trophoniella rudis
(Grube & Müller *in* Grube, 1877) n. comb.
(Fig. 25)

Stylarioides rudis Grube & Müller *in* Grube, 1877: 67, 71 (diagnosis). — Hartwich 1993: 134 *partim*.

Siphonostomum cariboum – Treadwell 1901: 208 *partim* (*non* Grube & Ørsted *in* Grube 1859).

Piromis sp.? – Nonato & Luna 1970: 90, 91, fig. 78.

TYPE MATERIAL. — **Southwestern Atlantic Ocean**. 3 syntypes of *Stylarioides rudis* (ZMB Q4791), off Florianopolis (*olim* Desterro), Santa Catharina Island, Brazil, F. Müller, 1 slide made from the former (ZMB 69146-01(5)), with some bubbles, contains few noto- and neurochaetae.

ADDITIONAL MATERIAL. — **Southwestern Atlantic Ocean**. 1 specimen (MNHN A183) slightly damaged, Abrolhos Archipelago (17°45'S, 38°50'W), 20 m, 1883, M. Parfait (16 mm long, 2.5 mm wide, cephalic cage 6 mm long, broken, 60 chaetigers).
Gulf of Mexico. 1 specimen (USNM 1156948), breaking

in 2, off Pepperfish Key, Florida, R/V *Fish Hawk*, stn 7151, 5.5 fathoms, 7.XI.1901 (12 mm long, 2 mm wide, cephalic cage 4 mm long, 45 chaetigers).

Caribbean Sea. 1 specimen (LACM-AHF 2500), pale, Allan Hancock Atlantic expedition, stn A14 (12°11'55"N, 72°11'03"W → 12°11'20"N, 72°11'16"W), 2 miles SW Cape La Vela, Peninsula La Guajira, Colombia, 22-21 fathoms, gray sand, 8.IV.1939 (17 mm long, 2 mm wide, cephalic cage 4 mm long, 51 chaetigers). — 1 specimen (USNM 16164), broken in 2, Ensenada Honda, Culebra, Puerto Rico, during the U.S. Fish Commission Porto Rico expedition, 1898-99, R/V *Fish Hawk*, 11.II.1899 (17 [8 + 9] mm long, 3 mm wide, cephalic cage 2 mm long, 51 [28 + 23] chaetigers).

DISTRIBUTION. — Originally described from Florianopolis (27°30'S, 48°30'W), formerly called Desterro, Santa Catharina Island, Brazil, where most Müller's specimens came from, but there are no more data. The specimen studied by Nonato & Luna (1970), which seems to be conspecific, comes from northeastern Brazil (off NE Maceió, Alagôas, *c.* 40 m, in calcareous algae). The specimen from Florida, together with the other ones found in Puerto Rico and Colombia, extend the distribution into the Great Caribbean region.

DESCRIPTION

Syntypes one complete specimen (Fig. 25A), an anterior fragment (Fig. 25E; measurements in parenthesis below), and a non-matching posterior fragment (probably dissected by Grube to observe the anterior end). Body fusiform, tapering posteriorly, complete syntype 29 mm long, 5 (4) mm wide, cephalic cage 5 (7) mm long, 54 (29) chaetigers. Tunic mostly without sediment particles, some sand grains on anterior fragment (Fig. 25E); body wall solid brown. Body papillae abundant, most thin, small, fragile, digitate, leaving rounded, low scars on tunic, giving a very rugose profile; larger papillae fewer, cylindrical or clavate, fragile, placed along chaetal lobes and arranged in longitudinal rows (two dorsal, one lateral and four ventral ones).

Cephalic hood not exposed; anterior fragment with palps exposed; not dissected to avoid further damage.

Cephalic cage chaetae as long as ¼-⅙ body length, as long as, or longer than body width. Chaetigers 1-4 involved in the cephalic cage, chaetae arranged in short dorsolateral series, with about 7-8 noto- and 4-5 neurochaetae. Anterior dorsal margin of first chaetiger with a median trifid lobe, projected anteriorly (Fig. 25B, D). Anterior chaetigers with long papillae. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt, falcate anchylosed neurohooks start in chaetiger 5. Gonopodial lobes present in chaetiger 5, broken from the base, scar remains.

Parapodia lateral, poorly developed; chaetae emerge from the body wall. Median neuropodia ventrolateral. Noto- and neuropodia not forming long lobes; anterior parapodia with abundant long papillae. Median notopodia with 2-4 infrachaetal smaller papillae and 3-5 larger papillae (Fig. 25F). Neuropodia with 1-2 infrachaetal and 3-4 suprachaetal papillae.

Median notochaetae arranged in short transverse series, 7-8 notochaetae per bundle, about as long as ⅕ body width; all notochaetae multiarticulated capillaries, each with articles short basally, long medially and distally (Fig. 25F, insert). Neurochaetae multiarticulated capillaries in chaetigers 1-4, all articles short, in chaetiger 4 with falcate tip. Falcate anchylosed, darker neurohooks from chaetiger 5, feebly developed rings continued to about half the exposed part (Fig. 25G); neurohooks arranged in transverse series, or as an inverted J-pattern, 5-6 in anterior and posterior chaetigers, 6-7 in median chaetigers, each with short rings extending almost to the distal part, subdistally straight, tip falcate, entire.

Posterior end tapering to a blunt rounded tip (Fig. 25C); pygidium with anus terminal, with many long papillae; no anal cirri.

REMARKS

Trophoniella rudis n. comb. is closely allied to *T. reishi* n. sp. as both have an early start of anchylosed, unidentate neurohooks, and because their tunic has very few sediment particles, being apparently without any sediment particles. They differ by the relative basic body wall pigmentation and the cephalic cage length. Thus, in *T. rudis* n. comb., the body is solid brown, and the cephalic cage chaetae are 1.0-1.5 times longer than body width, whereas in *T. reishi* n. sp. the body is dark pink, with fine red spots or rarely pale, and the cephalic cage is twice as long as body width.

The short note by Müller (1858: 218) indicates that he saw living specimens and although he

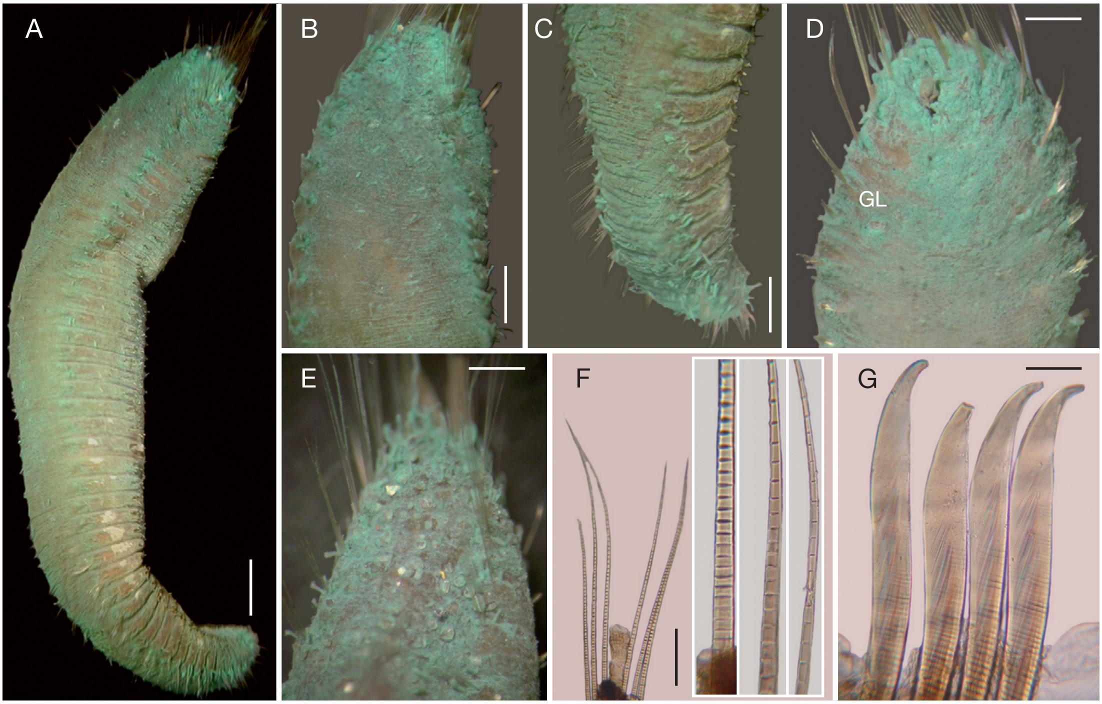

FIG. 25. — *Trophoniella rudis* (Grube & Müller *in* Grube, 1877) n. comb.: **A**, complete syntype (ZMB Q4791), lateral view; **B**, same, anterior end, dorsal view; **C**, same, posterior end, lateral view; **D**, same, anterior end, ventral view (**GL**, gonopodial lobes, broken); **E**, another syntype, anterior end, dorsal view; **F**, same, chaetiger 12, notopodium and basal, medial and distal notochaetal regions; **G**, same, chaetiger 29, neurochaetae. Scale bars: A, 2 mm; B, 1.35 mm; C, 0.7 mm; D, 1 mm; E, 0.8 mm; F, 225 µm; G, 73 µm.

commented that the "upper tentacles" were branchiae, he does not provide any other morphological details. The main diagnostic features for *Trophoniella rudis* n. comb. were: body with 60-74 chaetigers; papillae in two longitudinal rows dorsally and ventrally, one lateral row with longer, thinner papillae; cephalic cage made by chaetigers 1-4; neuropodia with four hooks per bundle; and branchiae cirriform, 24 filaments in a branchial plate distally notched. This series of characters resembles *Piromis* sp. as recorded by Nonato & Luna (1970); they stated that their specimen had gonopodial lobes in chaetiger 5, which were not included in the original diagnosis, but are visible in the largest syntype. The anterior end features could not be confirmed because of the state of the specimens; further, the discrepancy on the number of neurohooks may be explained by the then available microscopes, or because only the larger ones were seen or counted.

Trophoniella salazarae n. sp.
(Fig. 26)

TYPE MATERIAL. — **Eastern tropical Pacific**. Holotype (ECOSUR-116) and 1 paratype (MNHN), Careyeros (20°47'10" N, 105°30'48" W), Sayulita, Nayarit, Mexico, mixed shore, intertidal, 12.IV.2008, P. Salazar-Silva (paratype 82 mm long, 10 mm wide, cephalic cage 8 mm long, 112 chaetigers; gonopodial lobes not seen; 5 notochaetae in chaetiger 11). — 1 paratype (ECOSUR), Sayulita (20°52'15"N, 105°26'40"W), Nayarit, Mexico, mixed shore, intertidal, 28.XI.2004, P. Salazar & B. Yáñez (regenerating after 2 transverse bites, 1 in the posterior third of the body, the other in the last few chaetigers; 88 mm long, 5 mm wide, cephalic cage 8.5 mm long, 104 chaetigers; gonopodial lobes not seen; 5 notochaetae in chaetiger 11). — 1 paratype (UANL), broken in 2 matching pieces, Punta Cerritos (23°18'26.6"N, 106°27'21.3"W), Mazatlán, Sinaloa, Mexico, mixed shore, intertidal, 2.IV.2004, J. A. de León (92 mm long, 8 mm wide, cephalic cage 8 mm long, 105 chaetigers; gonopodial lobes not seen; 7 notochaetae in chaetiger 11). — 6 paratypes (UANL), 1 complete, 5 with the anterior end variously exposed, Punta Cerritos (23°18'26.6"N, 106°27'21.3"W), Mazatlán, Sinaloa, Mexico, mixed shore, intertidal, 22.III.2006, M. E. García & J. A. de León (complete one 69 mm long, 5 mm wide, cephalic cage 6 mm long, 98 chaetigers; gonopodial lobes not seen; 5 notochaetae in chaetiger 11).

Additional material. — **Eastern Pacific Ocean**. 2 juvenile specimens (ECOSUR), La Manzanilla (20°44'35"N, 105°23'14.8"W), La Cruz de Huanacaxtle, Nayarit, Mexico, 29.XI.2004, P. Salazar (5 mm long, 0.8-1.0 mm wide, cephalic cage 1.0-1.5 mm long, 34-42 chaetigers; first neurohooks in chaetiger 5; 4 notochaetae in chaetiger 11). — 2 specimens (LACM-AHF 2501), R/V *Velero IV*, stn 2603 (27°41'06"N, 114°53'38"W), 1.1 mile N-NE Kelp Point (Punta Sargazo), Port San Bartolomé (Bahía Tortugas), shore, rocks, 11.II.1954 (50-90 mm long, 8-10 mm wide, cephalic cage 11-12 mm long, 86-90 chaetigers). — 8 specimens (LACM-AHF 2502), San Quintin Bay, Baja California, Mexico, mud flats, 4.VII.1950, D. J. Reish (complete 76-82 mm long, 8-12 mm wide, cephalic cage 9-13 mm long, 75-98 chaetigers). — 1 specimen (USNM 1132096), broken in 2 pieces, Stony Island, Scammon Lagoon, Baja California, Mexico, 21.XII.1971, D. L. Bostie (68 mm long, 12 mm wide, cephalic cage 12 mm long, 82 chaetigers).

Type locality. — Playa Careyeros, Sayulita, Nayarit, Mexico.

Distribution. — The species has representatives in the eastern Pacific shores, from southern California and Baja California to Sayulita, Nayarit. It thrives in mixed beaches with rocky outcrops and sand, living within the sediments in intertidal to shallow subtidal depths.

Etymology. — This species is being named after Dr Patricia Salazar-Silva, friend and colleague, in recognition of her research on polynoid polychaetes, and especially because she collected some of the type specimens and kindly donated them to ECOSUR.

Description

Holotype (ECOSUR-116) blackish, club-shaped, many chaetae broken (Fig. 26A); body cylindrical, rounded, blunt anteriorly, tapering posteriorly, 91 mm long, 8 mm wide, cephalic cage (slightly broken) 8 mm long, 107 chaetigers. Tunic rugose, maculated, without sediment particles (Fig. 26B, C). Body papillae partially eroded, capitate, without sediment particles, short to very short (frequently eroded), arranged in three to four irregular, alternating transverse rows per segment (better seen in posterior chaetigers); longitudinal rows not visible; pigment in small rounded black spots of varying size.

Anterior end not exposed in holotype. Description based on paratypes (UANL) exposing their anterior end. Cephalic hood short, smooth, margin smooth. Prostomium low, pale. Eyes blackish. Caruncle blackish, well developed, extended along the full, branchial plate length; median keel blackish, lateral ridges pale, elevated (Fig. 26E). Palps pale, reddish-brown, thick, slightly longer than branchial plate, apparently depressed, with a cylindrical narrow stem and large, markedly ruffled, lateral wings (Fig. 26C, D). Lateral lips well developed, dorsal and ventral lips reduced; distorted into a flat plate in two paratypes. Branchiae pale, cirriform, sessile on a distally cleft, tongue-like protuberance, arranged in two lateral groups, in 7-8 parallel rows, with about 160 filaments per group; filaments longer basally, longest about as long as palps. Nephridial lobes pale, placed over the external, basal corner of the branchial plate.

Cephalic cage chaetae as long as body width. Chaetigers 1-2 involved in the cephalic cage; chaetae arranged in short dorsolateral, or lateral series, chaetiger 1 with 11 noto- and eight neurochaetae, chaetiger 2 with nine noto- and eight neurochaetae per side. Anterior dorsal margin of first chaetiger rounded, without projections (less contracted paratypes UANL with a short triangular projection, with small papillae). Anterior chaetigers with papillae of about the same size than those present throughout the body. Chaetigers 1-3 progressively slightly longer. Chaetal transition from cephalic cage to body chaetae abrupt; first anchylosed neurohooks present in chaetiger 5. Gonopodial lobes not seen.

Parapodia poorly developed, chaetae emerging from the body wall. Parapodia lateral, median neuropodia ventrolateral. Notopodia with two slighlty larger papillae, one basal, the other lateral, longest papillae about ⅕-⅙ as long as notochaetae. Neuropodia with papillae about as long as notopodial ones.

Median notochaetae arranged in short, transverse series, 7-8 notochaetae per bundle, about as long as ⅕-⅙ body width; all notochaetae multiarticulated, each with short articles in a small basal portion, then medium-sized, becoming markedly longer only distally (Fig. 26F, insert). Neurochaetae

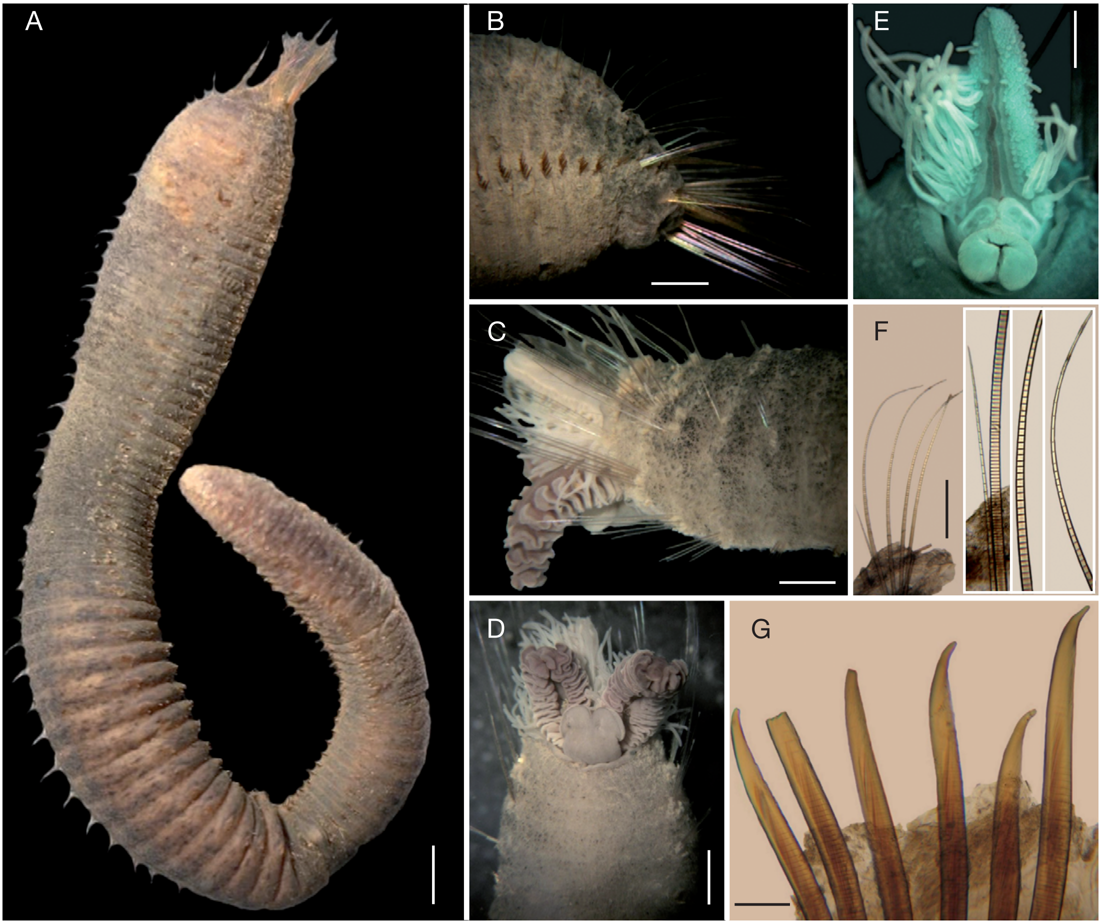

Fig. 26. — *Trophoniella salazarae* n. sp.: **A**, holotype (ECOSUR-116), lateral view; **B**, same, anterior end, lateral view; **C**, paratype (ECOSUR), anterior end, lateral view, head partially exposed; **D**, same, anterior end, frontal view; **E**, another paratype (UANL), head, frontal view, palps and many branchiae detached; **F**, holotype, chaetiger 12, notopodium (insert showing notochaetal basal, medial and distal regions); **G**, same, chaetiger 12, neurochaetae. Scale bars: A, 3.5 mm; B, 1.8 mm; C, 1.3 mm; D, 1.8 mm; E, 0.67 mm; F, 0.45 mm; G, 120 µm.

multiarticulated capillaries in chaetigers 1-4, falcate anchylosed neurohooks from chaetiger 5, arranged in transverse series (Fig. 26G), five per bundle in most chaetigers, only four in far posterior chaetigers, subdistally slightly expanded; short rings extending along ⅔-⅘ of the hook, blade paler, slightly compressed, thinner than handle, with tips slightly incurved, entire.

Posterior end tapering to a blunt, rounded lobe (Fig. 26A); pygidium with anus terminal, without anal cirri.

Variation

The juveniles resemble the adults by lacking any sediment particle over the body and by having a thin woolly layer surrounding individual papillae and neurohooks from chaetiger 5. The typical sensory papillae are arranged as four dorsal and four ventral papillae, forming longitudinal series. Furthermore, the palps are exposed in one juvenile and they are not foliose as in the adults; they are rather cylindrical with a well-developed midventral groove.

Remarks

Trophoniella salazarae n. sp. resembles *T. jareckiorum* n. sp. from the Caribbean Sea, as both have an opaque tunic without sediment particles. They differ especially regarding the tunic pigmentation, notochaetal number and type of articulation; thus, in *T. salazarae* n. sp. the tunic is blackish, whereas it is whitish in *T. jareckiorum* n. sp. There are more notochaetae in *T. salazarae* n. sp. (5-8 per bundle) than in *T. jareckiorum* n. sp. (4-5 per bundle), and the longer articles are restricted to the distal portion, whereas there are long articles in the median and distal portions of *T. jareckiorum* n. sp. notochaetae. On the other hand, *T. salazarae* n. sp. resembles *T. minuta* n. comb. but they differ in the number of notochaetae per bundle, being 7-8 in *T. salazarae* n. sp. and about 10 in *T. minuta* n. comb.

Trophoniella tumbensis
(Hartmann-Schröder, 1962) n. comb.
(Fig. 27)

Pherusa tumbensis Hartmann-Schröder, 1962: 153, 154, figs 199, 200. — Rozbaczylo 1985: 160. — Rozbaczylo & Moreno 2005: 122-124, fig. 1.

Type material. — **Southeastern Pacific Ocean**. Holotype of *Pherusa tumbensis* (ZMH 15441), NW Tumbes Peninsula (Talcahuano, Concepcion), Chile, in sand, with holothurians, 8.XII.1958, Jeldes (in label; in publication: Hulot).

Additional material. — **Central eastern Pacific Ocean**. An anterior fragment (LACM-AHF 2503), R/V *Velero III*, stn 69 (00°09'S, 91°23'W), Tagus Cove, Albermarle Island, Galápagos, rocky shore, tide pools, 11.II.1933 (58 mm long, 8 mm wide, cephalic cage 11 mm long, 50 chaetigers; first neurohooks in chaetigers 6 or 7, 1 on each side).

Distribution. — Originally described from the Tumbes Peninsula (Talcahuano, Concepción), Chile. Fauchald (1972: 414) wrongly listed Tumbes, Peru, as the type locality. The species has been found from Galápagos to southern Chile, in shallow-water sediments or in mixed bottoms.

Description

Holotype (ZMH 15441), without posterior end (Fig. 27A). Body grayish; fusiform, cylindrical, tapering posteriorly, 80 mm long, 9 mm wide, cephalic cage 12 mm long, 53 chaetigers. Tunic pale, with sediment cover dorsally (Fig. 27C), extending laterally, reaching neuropodia; ventral surface without sediment. Body wall black. Body papillae mostly eroded distally, dorsally difficult to see, ventrally arranged in four longitudinal rows or double papillar scars.

Anterior end not exposed; not dissected to avoid further damage.

Cephalic cage chaetae as long as body width. Chaetigers 1-4 involved in the cephalic cage; chaetae arranged as short dorsolateral series. Chaetiger 1 with 12 noto- and 10 neurochaetae, chaetigers 2-3 with 10 chaetae per bundle, chaetiger 4 with nine noto- and eight neurochaetae. Anterior dorsal margin of first chaetiger papillated, with a short, conical, bifid lobe, directed ventrally. Chaetigers 2-6 with two large dorsal papillae per segment, decreasing in size posteriorly, each as a rounded lobe, directed anteriorly. Chaetigers 1-3 of about the same length. Chaetal transition from cephalic cage to body chaetae abrupt; short, dark, anchylosed neurohooks start in chaetiger 7 (Fig. 27B, D). Gonopodial lobes not seen.

Parapodia poorly developed, chaetae emerging from the body wall. Parapodia lateral; median neuropodia ventrolateral. Noto- and neuropodia as short transverse slits carrying chaetae; notopodia with two postchaetal papillae, neuropodia with three smaller postchaetal papillae.

Median notochaetae arranged in short transverse series, 9-10 per bundle, as long as ¼-⅕ body width; all notochaetae multiarticulated capillaries, mostly broken distally, each with articles short, becoming slightly longer distally, tips falcate, hyaline (Fig. 27E, inserts). Neurochaetae multiarticulated capillaries in chaetigers 1-6; anchylosed neurohooks straight, dark brown, from chaetiger 7, arranged in transverse series, 5-6 per bundle (Fig. 27F), with short anchylosed articles or rings basally and medially, subdistally straight, blade pale, finely obliquely striated, tip entire, falcate, surface rough.

Posterior end unknown.

Remarks

Trophoniella tumbensis n. comb. is very similar to *T. americana* n. comb. There are two main differences between them: *T. tumbensis* n. comb. has more abundant notochaetae (8-10) than *T. americana*

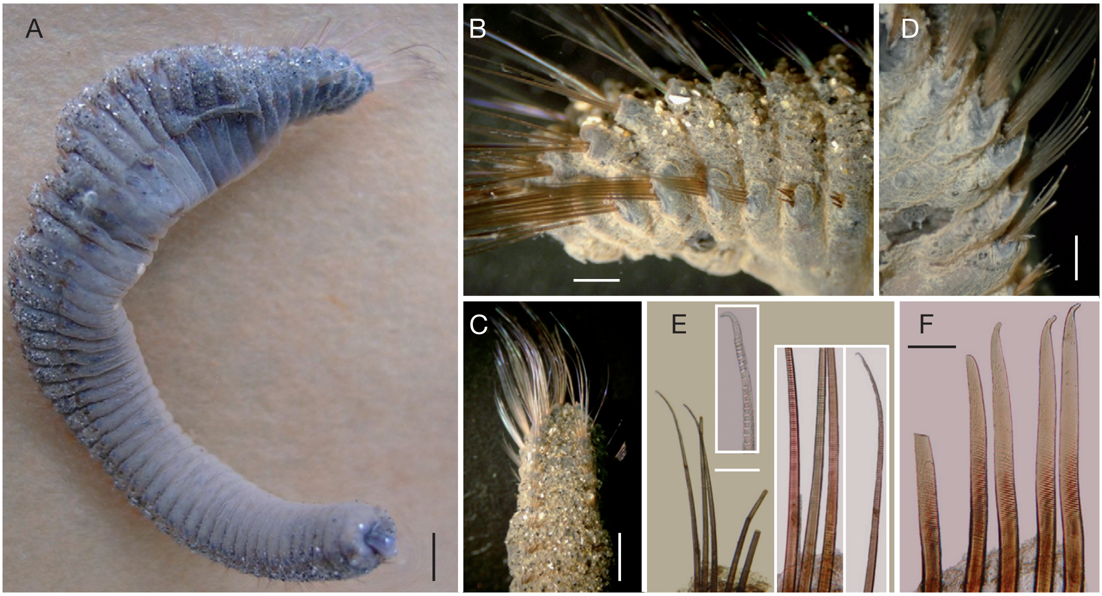

Fig. 27. — *Trophoniella tumbensis* (Hartmann-Schröder, 1962) n. comb., holotype (ZMH 15441): **A**, lateral view; **B**, anterior end, lateral view; **C**, anterior end, dorsal view; **D**, anterior end, ventral view, tunic removed to seek gonopodial lobes; **E**, chaetiger 13, notopodium (inserts: basal and distal notochaetal regions, and notochaetal tip); **F**, chaetiger 10, neurohooks. Scale bars: A, 2.6 mm; B, 1 mm; C, 2.3 mm; D, 1.5 mm; E, 100 µm; F, 45 µm.

n. comb (3-5), and its body wall is grayish, whereas it is pinkish or pale in *T. americana* n. comb.

In the original description (Hartmann-Schröder 1962: 154), it was stated that neurohooks start in chaetiger 8, but they actually start in chaetiger 7. The difference could be explained because one side of the anterior end of the holotype was regenerating, without many chaetae, and this could confuse the chaetiger count. The falcate notochaetae are detectable, when present, using the stereo microscope because their tips catch some foreign materials; however, many chaetae are broken and this feature was overlooked in the original description. Likewise, because the tips are so fragile, it would be of little use to emphasise their usage as a diagnostic or key feature.

Trophoniella sp. Brazil

Pherusa sp. – Rullier & Amoureux 1979: 183.

Material examined. — **Southwestern Atlantic Ocean, Brazil.** 2 specimens (MNHN 884), damaged, many chaetae broken, previously dissected, Rocas Island, R/V *Calypso*, stn 6, 7-8 m depth, 17.XI.1961 (12-17 mm long, 1.5-2.0 mm wide, cephalic cage 3.0-3.5 mm long, 55-57 chaetigers).

Diagnosis. — Tunic with large, white particles dorsally, extended laterally and ventrally, being smaller ventrally and less densely packed posteriorly. Dorsal and parapodial lobes missing. Four or five notochaetae per bundle. First anchylosed neurohooks from chaetiger 5, tips entire. Branchiae pale with a blackish subdistal dot.

Distribution. — Only known from the Rocas Island, off Brazil.

Remarks

As indicated in the key above, this new species is closely allied to *T. rigida* n. comb. They differ in the relative colour and density of particles, and on the type of neurokooks. Thus, the new species has whitish, very abundant particles and entire neurohooks, whereas *T. rigida* n. comb. has mostly blackish, sparse particles, and furcated neurohooks. Formal description requires better specimens and should be postponed until they are either collected or made available.

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This series of revisions on flabelligerid polychaetes started during my sabbatical leave. I wholeheartedly thank Kristian Fauchald and Len Hirsch (USNM), Leslie Harris and David Ocker (LACM) and Patrick Gillet (IRFA) for their warm support and housing facilities. Further, this research was kindly supported by many colleagues, curators and collections managers and their efforts are much appreciated: Alejandro Tablado (MACN), Angelika Brandt and Gisela Wegener (ZMH), Ardis Johnson (MCZ), Barbara Mikac, Birger Neuhaus (ZMB), Chris Glasby (NTM), Danny Eibye-Jacobsen (ZMUC), Dieter Fiege (SMF), Elin Sigvaldadottir and Karin Sindemark (SMNH), Emma Sherlock and Miranda Lowe (BMNH), Fredrik Pleijel (then in MNHN), J. Angel de León-González (UANL), Joke Bleeker and Harry Ten Hove (ZMA), Goeff Keel (USNM), Kathy Omura and Kirk Fitzhugh (LACM), Marie-Noëlle Helleout and Tarik Meziane (MNHN), Mark Siddall (AMNH), Nancy Voss (UMML), Norma Emilia González (ECOSUR), Patrick Gillet (IRFA), Robert Van Syoc (CAS). The critical reading by Danny Eibye-Jacobsen (ZMUC), Philippe Bouchet and Annemarie Ohler (MNHN) resulted in a much improved version. Funds for this research were provided by ECOSUR, the USA Department of the Interior, Fulbright Commission, the IRFA and Conacyt (Fund 61609).

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